Universidade de Aveiro Departamento de Biologia
2015

Alexandre Stefano Sousa Ramos

Early post-fledgling survival in a fragmented population of a tropical cooperative breeding passerine

Esperança de vida de crias de um passeriforme com reprodução cooperativa numa população fragmentada de uma zona tropical

DECLARAÇÃO

Declaro que este relatório é integralmente da minha autoria, estando devidamente referenciadas as fontes e obras consultadas, bem como identificadas de modo claro as citações dessas obras. Não contém, por isso, qualquer tipo de plágio quer de textos publicados, qualquer que seja o meio dessa publicação, incluindo meios eletrónicos, quer de trabalhos académicos.

Universidade de Aveiro Departamento de Biologia
2015

Alexandre Stefano Sousa Ramos

Early post-fledgling survival in a fragmented population of a tropical cooperative breeding passerine

Esperança de vida de crias de um passeriforme com reprodução cooperativa numa população fragmentada de uma zona tropical

Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia Aplicada, realizada sob a orientação científica do Doutor Amadeu Mortágua Velho da Maia Soares, Professor catedrático do Departamento de Biologia da Universidade de Aveiro

Agradecimentos

Há três anos fiz o *check-in* de um voo que acabaria por ter dois destinos muito diferentes. Um, o mais imediato, para Bruxelas. O outro, para um novo mundo que acabar por me mostrar o que até então desconhecia. A nível profissional, o objetivo desta viagem foi o de fazer um estágio curricular no laboratório de ecologia terrestre da universidade de Gent e para isto, disporia (apenas) de um ano. Tão curto pareceu o tempo que lá estive que decidi(mos) começar o mestrado que agora terminou com a apresentação da tese.

Muitas histórias há para contar destes três anos. Os mais variados sentimentos fizeram parte do meu dia-a-dia, emoções difíceis de explicar mesmo para quem as experienciou.

Neste percurso, foram incontáveis as pessoas que direta ou indiretamente me ajudaram a concluir esta importante fase, no entanto gostaria aqui de fazer uma pequena referência aos indispensáveis.

Antes de tudo gostaria de agradecer ao Prof. Dr. Amadeu Soares por 3 anos atrás me ter dado a oportunidade de integrar um dos melhores departamentos em ecologia da Europa. Este ato foi essencial para tudo o que veio no seguimento deste evento. Por outro lado, numa fase em que as dificuldades foram muitas, o prof. Amadeu mostrou um elevado sentido de respeito e compreensão que só uma pessoa com elevado intelecto é capaz de ter.

With Portugal behind, Prof. Dr. Luc Lens walked me on TEREC and showed me the so far unknown scientific world. From the first moment, his professionalism, intelligence and good character guide me throughout the years and were an example that I tried to follow. I would like here to publicly acknowledge the trust he placed on me to go to Kenya and integrate the great Taita Hills project. Besides, he was always available to solve problems or to clarify some doubts that arose during this long process.

An also important piece during this journey was Dries van de Loock, especially during the field work in Taita Hills. Furthermore, I would like to thank him for his dedication, time and energy spent between correcting texts and R codes, someone had to do it and he was the one!

Dr. Liesbeth de Neve had a major role during the planning and preparation of all the field work therefore I would to leave here a big thank

An also important piece during this journey was Dries van de Loock, especially during the field work in Taita Hills. Furthermore, I would like to thank him for his dedication, time and energy spent between correcting texts and R codes, someone had to do it and he was the one!

Dr. Liesbeth de Neve had a major role during the planning and preparation of all the field work therefore I would to leave here a big thank you.

One of the most challenging part of my thesis were the statistical analyses. Here, I must mention two great researchers, Diederik Stubbe and Maxime Dahirel. Their support was critical in order to have the right results.

Hans Matheve, thank you for all ptilochronology scannings and small chats that broke hours and hours straight on the computer.

During the two months of field work in Taita there were, naturally ups and downs. There, Lawrence Wagura went from a colleague to a good friend that made me see Kenya with a different eyes.

Por vezes, uma palavra, um gesto, um sinal ou simplesmente um olhar quebra a frágil ligação existente entre duas formas ditas racionais. Racionalismo este tão apreciado pelas suas maravilhosas implicações mas que silenciosamente nos priva de emoções, oportunidades ou até mesmo experiências. Quão fortes são então as relações pessoais que dia após dia criamos/destruímos? Serão as amizades então baseadas num baixo grau de racionalismo usado por cada interveniente? Será por isso tão seletivo o grupo de indivíduos a quem chamamos “amigos”? Obrigado Fred por sempre teres dado a uma palavra, gesto, sinal ou olhar o insignificante valor que acabam por ter.

También me gustaría hacer una pequeña referencia a Parto y Ronny, mis grandes compañeros de casa. Gracias por la paciencia, los platos lavados, la casa ordenada, la grapa guardada para mi y por todos los otros grandes momentos que pasamos en nuestro castillo!

To the Polé Polé crew a special thank you for all the nice crazy moments that decreased my stress levels ☺

A todos os restantes conhecidos, amigos e familiares um muito obrigado pelo apoio e energia positive que depositaram em mim.

Por último mas não menos importante gostaria de agradecer à

To the Polé Polé crew a special thank you for all the nice crazy moments that decreased my stress levels ☺

A todos os restantes conhecidos, amigos e familiares um muito obrigado pelo apoio e energia positive que depositaram em mim.

Por último mas não menos importante gostaria de agradecer à minha família pelo apoio incondicional dia após dia. Foi um prazer ter partilhado por telefone com vocês o momento em que acabei esta tese. O amor que sinto por vocês é único e eterno!

Palavras-chave

Reprodução cooperativa, floresta tropical, Cabanis's greenbul, Taita Hills, ptilocronologia, qualidade do individuo/habitat, radio-telemetria

Resumo

Ao longo dos últimos anos, a floresta tropical tem sido alvo de intenso estudo, especialmente devido à sua destruição em grande escala. Embora ainda haver muito ainda por explorar, já começamos a perceber quão negativo pode ser o impacto de nossas ações neste ecossistema.

Por conseguinte, certas comunidades têm vindo a desenvolver estratégias para superar este problema evitando diminuição das populações ou até mesmo extinções locais.

Reprodução cooperativa (RC) foi recentemente apontou como uma dessas estratégias. RC é um sistema reprodutivo em que dois ou mais indivíduos criam uma ninhada. A maioria dos indivíduos extras são crias de anteriores ninhadas que atrasam a sua dispersão e reprodução independente o que lhes permite ajudar os pais a criar os seus irmãos na época de reprodução subsequente. Acredita-se que tal comportamento possa ser devido, por exemplo, à falta de companheiros ou territórios de reprodução (hipótese das restrições ecológicas), uma consequência da fragmentação e / ou perturbação do habitat. A partir deste ponto, RC é facilmente promovida se o sucesso reprodutivo do grupo é maior que o de casais indivíduos isolados.

Assim sendo, nesta tese explorei a sobrevivência das crias no período após saída do ninho de uma espécie de passeriforme com RC. Nomeadamente o impacto da qualidade do individuo/habitat na sua probabilidade de sobrevivência durante o período de dependência das crias.

A espécie em causa é o Cabanis's greenbul (Phyllastrephus cabanisi) (PC), um passeriforme acastanhado de médio porte, classificada dentro da família Pycnonotidae. Pode ser encontrada na África Central em países como Angola, República Democrática do Congo, Moçambique e Quénia, habitando vários tipos de florestas primárias e secundárias, até 2700m de altitude. Estudos anteriores concluíram que PC é um reprodutor cooperativo facultativo.

Este estudo teve lugar em Taita Hills (TH) nas "East Arc Mountain" (EAM), uma cadeia de montanhas que vão de sudeste Quênia ao sul da Tanzânia. TH compreende uma área de 430 ha e devido à intensa desflorestação, 98% da floresta desapareceu nos últimos 200 anos. Hoje em dia a sua floresta está dividida em fragmentos sendo o nosso estudo baseado em 5 desses fragmentos.

A sobrevivência das crias foi obtida por rádio-telemetria através das fêmeas reprodutoras (FR).

Ptilocronologia é o estudo de barras crescimento das penas e tem sido utilizado para estudar o estado nutricional de uma ave. Esta técnica considera que a taxa de crescimento da pena é positivamente proporcional à capacidade individual de ingestão de alimentos e da disponibilidade alimentar. Esta técnica é utilizada para inferir, portanto, para a qualidade individual / habitat.

A sobrevivência foi menor durante os primeiros 5 dias após saída do ninho, cerca de 53,3%. Durante os 15 dias seguintes, o risco de morte diminuiu para 14,3%. Isto representa um total de sobrevivência de apenas 33% no final dos 50 dias.

Os nossos resultados mostraram ainda uma relação significativamente positiva entre o tamanho do grupo reprodutivo e a sobrevivência das crias, bem como entre os valores ptilocronologia e a probabilidade de sobrevivência das crias. Na prática, isto significa que quanto maior o grupo reprodutivo, maior a sobrevivência das crias e que quanto melhor for a qualidade do habitat ou de fêmea reprodutora, maior será a taxa de sobrevivência. Isto leva-nos a crer que a RC é um comportamento adaptativo no sentido de compensar pela falta de companheiros/território reprodutivo originado pela destruição da floresta e perturbação.

Tais resultados confirmam a importância da qualidade do habitat na sobrevivência das crias, e ainda, pela primeira vez demonstra como o tamanho do grupo reprodutivo influencia a probabilidade de sobrevivência dos juvenis e consequentemente a dinâmica populacional desta espécie.

Na minha opinião, futuros estudos devem tentar separar a qualidade do habitat e a qualidade do individuo bem como verificar que relação existe entre eles. Isto vai-nos ajudar a entender melhor que fator tem mais impacto na sobrevivência das crias e, portanto, redirecionar os nossos estudos nessa direção.

A fim de confirmar o impacto negativo da perturbação humana e fragmentação da floresta, seria de grande relevância comparar as estratégias reprodutivas e o sucesso reprodutivo das populações que vivem nas florestas intactas VS floresta perturbada.

Key-words

Cooperative breeding, tropical forest, Cabanis's greenbul, Taita Hills, ptilochronology, individual/habitat quality, radio-telemetry

Abstract

During the last years tropical forest has been a target of intense study especially due to its recent big scale destruction. Although a lot still needs to be explored, we start realizing how negative can the impact of our actions be for the ecosystem.

Subsequently, the living community have been developing strategies to overcome this problem avoiding bottlenecks or even extinctions.

Cooperative breeding (CB) has been recently pointed out as one of those strategies. CB is a breeding system where more than two individuals raise one brood. In most of the cases, extra individuals are offspring that delay their dispersal and independent breeding what allows them to help their parents raising their siblings in the subsequent breeding season. Such behavior is believed to be due, per example, to the lack of mates or breeding territories (*ecological constraints hypothesis),* a consequence of habitat fragmentation and/or disturbance. From this point, CB is easily promoted by a higher reproductive success of group vs pairs or single individuals.

Accordingly, during this thesis I explore the early post-fledging survival of a cooperative breeding passerine, namely the impact of individual/habitat quality in its survival probability during the dependence period of the chicks.

Our study species is the Cabanis's greenbul (*Phyllastrephus cabanisi*), a medium-sized, brownish passerine, classified within the *Pycnonotidae* family. It is found over part of Central Africa in countries such as Angola, Democratic Republic of the Congo, Mozambique and Kenya, inhabiting primary and secondary forests, as well as woodland of various types up to 2700m of altitude. Previous studies have concluded that PC is a facultative cooperative breeder.

This study was conducted in Taita Hills (TH) at the Eastern Arc Mountains (EAM), a chain of mountains running from Southeast Kenya to the South of Tanzania. TH comprises an area of 430 ha and has been suffering intense deforestation reflecting 98% forest reduction over the last 200 years.

Nowadays its forest is divided in fragments and our study was based in 5of those fragments.

We access the post-fledging survival through radio-telemetry. The juvenile survey was done through the breeding females in which transmitters were placed with a leg-loop technique.

Ptilochronology is consider to be the study of feather growth bars and has been used to study the nutritional state of a bird. This technique considers that the feather growth rate is positively proportional to the individual capability of ingesting food and to the food availability. This technique is therefore used to infer for individual/habitat quality.

Survival was lowest during the first 5 days post-fledging representing 53.3%. During the next 15 days, risk of predation decreased with only 14.3% more deceased individuals. This represents a total of only 33% survived individuals in the end of the 50 days.

Our results showed yet a significant positive relationship between flock size and post-fledging survival as well as between ptilochronology values and post-fledgling survival. In practice, these imply that on this population, as bigger the flock, as greater the post fledging survival and that good habitat quality or good BF quality, will lead to a higher juvenile survival rate. We believe that CB is therefore an adaptive behaviour to the lack of mates/breeding territory originated from the mass forest destruction and disturbance.

Such results confirms the critical importance of habitat quality in the post-fledging survival and, for the first time, demonstrates how flock size influences the living probability of the juveniles and therefore how it impacts the (local) population dynamics of this species.

In my opinion, future research should be focus in disentangle individual and habitat quality from each other and verify which relationship exist between them. Such study will allow us to understand which factor has a stronger influence in the post-fledging survival and therefore redirect our studies in that direction. In order to confirm the negative impact of human disturbance and forest fragmentation, it would be of major relevance to compare the reproductive strategies and reproductive success of populations living in intact forests and disturbed patches.

Table of Contents

Introduction

Tropical forest ecosystems host more than two-thirds of the Earth's terrestrial biodiversity which provides significant local, regional and global human benefits (Bradshaw, 2009; Gardner, Barlow et al., 2009). Despite its value, ongoing deforestation and fragmentation of tropical forests are the most commonly-cited reasons for the decline of avian populations and the loss of biodiversity (Robinson, 1995). The persistent and cumulative effects of habitat loss and fragmentation, over-harvesting, the introduction of invasive species and global environmental changes make tropical forests an epicenter of current and future extinctions (Bradshaw, 2009; Gardner, Barlow et al., 2009). *In situ*, all these factors lead to landscape changes, such as reduced fragment-matrices and interior-edge ratios. Furthermore, these landscape changes are argued to increase the pressure from surrounding predators, competitors, parasites and diseases (ROLSTAD, 1991). Therefore, these environmental fluctuations are likely to be important drivers of selection pressures and are expected to impact the evolution of behavioral, morphological and physiological traits, including cooperation (Cockburn and Russell, 2011; Callens, 2012).

Cooperative breeding is a breeding system in which one or more individuals regularly forgo the opportunity to breed independently and instead breed cooperatively with other conspecifics, either as non-reproductive `helper' or as co-breeder (Arnold and Owens, 1998).

Previous studies have suggested that individual quality assessment has been very poorly integrated into cooperative breeding studies. Therefore, it is essential to understand the significance of physiological state or external circumstances on reproductive decisions and success when studying the evolution and persistence of cooperative breeding behavior.

Current understanding of Cooperative Breeding

Kin-based and non kin-based societies

Different evolutionary routes might lead a population to a certain cooperative system, which can be divided in kin-based or a non-kin-based societies.

In one hand, kin-based societies implicates that offspring delay their dispersal and help their parents in raising siblings of one or more consecutive broods, independently if they also delay their reproduction or not. Recent comparative work in both invertebrates and vertebrates suggests that high relatedness among group members may be critical to the evolution of complex animal

societies. However, despite the great importance of this subject to explain the evolution of family groups, relatedness alone is not sufficient to explain many individual differences in reproductive strategies (Rubenstein, 2011).

In another hand, non kin-based societies are rarer and more difficult to explain because kin selection cannot maintain their cooperative interactions (Riehl, 2013). High rates of adult mortality, copulations outside the social group, or conspecific brood parasitism can eliminate genetic relatedness to such low levels that the indirect fitness benefits of helping are negligible. Some of this behaviour were already described in particular animals inclusive on fairy-wrens (*Malurus* spp.) in which apparent 'family' groups often contain step-parents and extra-pair young (Dunn, Cockburn et al., 1995).

Another possible process that might explain non kin-based societies was described on Ione birds (usually males) that join unrelated pairs or groups on its breeding territory hoping to have an extra-pair copulation with the resident female (Riehl, 2013).

Ultimately, cooperative polygamy might occur when two or more unrelated individuals (typically of the same sex) form a cooperative coalition, establish or take over a breeding territory together, and then share reproduction and parental care in a single clutch. This behaviour can be observed for example in the Brown Skuas (*Catharacta lonnbergi) (Young, 1998).*

Main explanatory hypotheses

Ecological constraints, such as high dispersal costs and shortage of territory vacancies, breeding partners or food availability, have all been identified as important factors that force individuals not only to delay dispersal, but also to delay their independent breeding (*ecological constraint hypothesis)* (Hatchwell and Komdeur, 2000; Walter D. Koenig, 2004). Ecological factors certainly help to explain the occurrence of cooperative breeding within species (Hatchwell, 2009), but failed to do so between species. Comparative studies showed that slow life-history trades (i.e. low adult mortality, low fecundity, slow development) better explain the variation in the occurrence of this behavior among species. This is predicted by the so called *life history hypothesis* (Owens, 1998). Covas and Griesser (2007) suggest that longevity favors a delayed of reproduction and gives parents the opportunity of a prolonged investment in offspring, an option which is not available for short-lived species (Covas and Griesser, 2007). Individual variation in strategies to increase survival might be linked then to individual quality. Moreover, if high-quality individuals

compete more effectively for superior reproductive vacancies, their mates will also tend to be in superior condition. This is thought to augment the benefits of staying home where high-quality territories and individuals are clumped, leading to a delay in dispersal (Stacey, 1987; Walter D. Koenig, 2004).

On the other hand 'delayers' might be birds of poor quality, unable to breed independently. As such, the costs of staying on the natal territories as well as delaying independent breeding are lower than dispersing away from the natal territory and having a failed breeding attempt (Walter D. Koenig, 2004).

While there are numerous studies providing evidences that support the idea that constraints on dispersal, habitat quality or mate limitation promote group living, in a significant number of other species the existence of constraints on dispersal are unclear or even unlikely (Clutton-Brock, 2002; Griesser, Nystrand et al., 2006; Sorato, Gullett et al., 2012).

Moreover, it was proposed that *benefits of group living* might explain the evolution of sociality, at least partially (Sorato, Gullett et al., 2012). Using this strategy, groups might have advantage over individuals because the first might be more adapt, p. e. at finding and foraging for food as well as at detecting or evading predators (Davies and Krebs, 1993).

Finally, the *skill hypothesis* suggests that offspring may remain associated with parents to gain the skills required for independent survival and reproduction (Langen, 1996). However, this latter hypothesis lacks consensus once that it is difficult to disentangle effect of individual quality from acquired skills/experience necessary for their reproductive success (Walter D. Koenig, 2004).

Recently, Rubenstein (2011) proposed that helping behavior maximizes fitness not by increasing the overall reproductive success of groups, but by reducing fecundity variance and thus minimizing the probability of reproductive failure. Such a *bet-hedging* strategy is particularly plausible when there are high temporal or spatial variation conditions, once that the probability of reproductive failure during those events is high (Rubenstein, 2011).

From the parent perspective, they can benefit from the presence of helpers in one of two ways: or by reducing their own feeding frequencies *(load-lightening hypotheses*) (Walter D. Koenig, 2004; Crick, 1992) or by increasing their reproductive output (*additive effect*). Load-lightening strategy implies that the breeding pair reduces their reproductive effort and save resources that might improve their survival allowing, in a long-term, a higher lifetime reproductive success, possibly avoiding negative effects for the chicks (Santos and Macedo, 2011). On the other hand, if the contribution of the helpers supplements the effort done by the parents, hereby decreasing

nestling starvation risks and/or increasing the survival chances of the fledglings of a particular clutch, the helper effect is called *additive* (Blackmore and Heinsohn, 2007; Kingma, Hall et al., 2010).

Parents on good territories (good nutritional condition) can also allow helpers to stay during the next breeding season, because there is enough food for everyone. Therefore, the conflict helpers vs. breeders will be small in good territories, and parents can benefit from the help on their next breeding attempt, thereby increasing their fitness (Walter D. Koenig, 2004; Crick, 1992).

On the other hand, if 'outside' conditions are bad, helpers may benefit to stay to help and wait to the next season to disperse and breed by themselves. The benefits of staying would be to increase survival probability by living in groups (*group augmentation hypotheses*), to help raise siblings (indirect fitness benefits) and to gain breeding experience, so that the chance of being successful in the future would be larger (Hanna Kokko, 2001; Walter D. Koenig, 2004).

Cabanis's Greenbul in Taita Hills

For more than 20 years that Taita Hills, Kenya has been a target area for several avian studies. This is true particularly for our model species, the Cabanis's greenbull (CG) (*Phyllastrephus cabanisi*).

This species currently ranks among the best studied forest birds in sub-Saharan Africa (Husemann, Cousseau et al., 2015) and has been subject of different studies, among others, demographic and genetic population structure, impact of habitat disturbance and influence of predation on the population dynamics (Callens, Galbusera et al., 2011; Aben, Adriaensen et al., 2012; Spanhove, Callens et al., 2013; Vangestel, Callens et al., 2013). In 1999, Luc Lens compared historical (museum specimens) and current levels of FA in tarsus length and concluded that *P. cabanisi* are very sensitive to forest degradation. In 2002, the same author showed that together, dispersal rate and change in asymmetry explained 88% of the observed variation in patch occupancy between the studied species, with each factor contributing equally to this relationship (Lens, Van Dongen et al., 2002).

Video-taping of nests in Taita Hills revealed that in more than 10% of the nests, helpers were present (Callens, 2012). This classifies the Cabanis's greenbul as a cooperative breeder. Since then, this particular social breeding system has been the focus of continued research in the Taita Hills.

Genetically, Carl Vangestel et. al (2013) found evidences of female-biased dispersal at small spatial scales. At a landscape level, individual-based autocorrelation values decreased over time while levels of admixture increased, possibly indicating increased gene flow over the past decade (Vangestel, Callens et al., 2013).

Recently, M. Husemann et. al, (2015) showed that, contrary to the expectations, effective population size slightly increased. This might suggest that Cabanis's greenbul are increasingly coping with fragmentation, although the time period over which these trends were documented is rather short relative to the average longevity of tropical species (Husemann, Cousseau et al., 2015).

Territory quality and environmental stress level

Ptilochronology

Variation in habitat/individual quality can profoundly affect the survival and reproduction of birds (ALAN B. FRANKLIN, 2000)

For researchers interested in indirect measures of habitat quality, individual nutritional condition may be a particularly sensitive way of assessing how the environment affects birds over short periods of time. Nutritional-condition can be measure through such indicators as body mass, fat deposits, blood metabolites, hormone levels, and/or analyses of the growth bars on feathers (ptilochronology) (Elderbrock, Kern et al., 2012).

An organism ability to reproduce and survive (individual quality) may depend on its size and its condition where condition might include, among other things, territory quality, fat reserves, protein reserves, foraging skills, parasite loads and the state of its immune system (McNamara, 1996; Wendeln, 1999). Individuals typically differ in features like the previously mentioned ones (Wendeln, 1999). Territory quality is intimately connected with the general perspective of individual quality being both dependent on each other. This fact makes then very difficult to disentangle and therefore both will be consider here as an approximation of one another.

This technique is mostly considered to be an unambiguous index of nutritional condition (Grubb, 2006). We assume that energy is a limiting factor and that any life form allocates primarily the required amount of energy for maintenance and for reproduction. Furthermore, natural selection has favored the regeneration of lost body parts as rapidly as possible, independently of their body mass or fat content (Grubb, 2006). Birds in particular are considered to be very

vulnerable to predation during molt and therefore are expected to reduce such periods to the minimum (Vangestel, 2011). The more energy the bird is able to allocate in the feathers growth, the faster they grow, leading to wider growth bars. Such feature is a blueprint that allows researchers to infer about defense skills, social behavior or even reproductive effort (Grubb, 2006). On this study, we used ptilochronology measurements on tail feathers to assess habitat/individual quality based on the nutritional conditions of each specimens (Grubb, 2006).

Ptilochronology is the study of feather growth bars and has been used to study the nutritional state of a bird (Frasz, Fischer et al., 2013). This technique has been extensively applied in the literature since it was discover by Thomas Grubb in 1989. Besides the bird's nutritional condition, it has a direct relationship with environmental quality, survival probabilities, reproduction outcome, parental care, sibling competition, etc. (Grubb, 2006; Vangestel, 2011; Fehérvári, Solt et al., 2014). Although the exact mechanism responsible for the growth bars are yet to explain, Grubb (2006) suggests that the dark and light color is associated with the different orientation of the vane relative to the shaft or rachis of the feather. The same author explains that this different orientation of the vane creates a subtle undulation on the feather surface that gives rise to the feather growth bars (Grubb, 2006).

Fluctuating asymmetry (FA)

More and more, ecosystems suffer external pressures through a variety of activities that, among others, increase rates of species invasions, reduce suitable habitat, decrease population's size, restrict gene flow and species extinctions (Lens, 1999; Hooper, Chapin et al., 2005). These perturbations highly increase the biota stress level causing hormonal (Okuliarova, Sarnikova et al., 2010), behavioural, physiological and morphological changes (Drummond and Ancona, 2015). Over the last decade, ecologists have been trying to measure the impact of this environmental and genetic stress on the developmental stability (DS) of single populations or communities. Fluctuating asymmetry has been proven to be a simple and effective method to be used (Lens, 1999). FA is defined as the randomly directed deviations from perfect symmetry that would be expected in bilateral structures if individuals would have the perfect control of its morphological development (Lens, 1999). It has been suggested that "FA reflects an animal's ability to cope with the sum of *challenges* during its growing period" (Knierim, Van Dongen et al., 2007).

Through the years, numerous studies have used FA as an indicator of developmental stability and most of them shown that environmental or genetic stresses interferes with the precise regulation of development processes resulting therefore in an increase of FA (Witter, 1994; Fair, Hansen et al., 1999; Talloen, Lens et al., 2008).

Fluctuating asymmetry, although is the most used method to calculate development instability (DI), it represents only one of three types of asymmetry. They can be distinguished by the different distributions that their results compose as well as its mean and variance (Palmer, 1986; Lens and Van Dongen, 2000). Directional asymmetry reflects a consistent pattern of a trait within a species towards greater development on one side of the body than on the other (normal distribution with nonzero mean). Antisymmetry represents a pattern towards greater development of one side of the body than the other, although it occurs approximately in equal frequency on both sides (bimodal distribution with zero mean). A good example is the male fiddler crabs that has one oversized claw and it occurs with approximately the same frequency on left and right sides. FA differs from the previous two once that represents situation with normal distribution with and a zero mean (Palmer, 1986; Lens and Van Dongen, 2000).

Post-fledging survival

The post-fledging period is the time between the offspring leaving the nest (fledging) and natal dispersal (Tarwater and Brawn, 2010). This period is considered by many authors as critical in order to explain fundamental life-history differences between tropical and temperate-zone species and for understanding population dynamics of birds (Sandercock, Beissinger et al., 2000).

Until now, most studies of avian survival have been conducted in temperate regions, while little is known about factors affecting survival and population sizes of tropical birds (Sankamethawee, Gale et al., 2009).

In 2009, Sankamethawee *et al.* studied the post-fledging survival of the cooperatively breeding Puff-throated Bulbul (*Alophoixus pallidus*) in an evergreen forest in north-eastern Thailand and found out that the probability of surviving the 8-week period of dependency was 0.61 ± 0.09 (Sankamethawee, Gale et al., 2009). Furthermore, Tarwater et al. (2011) estimated survival until reproduction, age at first reproduction, and sources of variation in juvenile survival in neotropical passerine Western Slaty-antshrike (*Thamnophilus atrinucha*), in central Panama. They concluded

that fledged antshrikes had 76% survival through the dependent period and that survival rate was lowest during the first week after leaving the nest (Tarwater, Ricklefs et al., 2011).

Currently, because of the absence of realistic data, annual survival of juvenile passerines is frequently estimated at 0.31 or half of adult's survival. Recent studies suggest that fledgling's survival varies dramatically by species and region and survival during the first weeks after fledging can be lower than conventional estimates (Hatchwell, 2009; Vitz and Rodewald, 2011).

Understanding factor affecting survival, lead us to a greater knowledge of how to identify and explain evolutionary adaptations and elucidate potential mechanisms of population decline (Yackel Adams, Skagen et al., 2006).

Aims

Firstly, we would like to infer how territory/individual quality and stress levels vary among fragments. This would give us already some information about how each fragment is being affected by the existing external factors (changing its habitat quality) or how are the different meta-populations influenced by it. Once that no previous habitat quality assessment was performed on the fragments analysed in this study, it is difficult to predict an effect. In one hand the differences in habitat quality might be big enough to be represented in the BF tail feathers growth bars or, in another hand, once that our study was conducted in Kenya, a tropical region characterized by a more constant food availability, we might not see consistent differences among individual tail feathers. Although, it is important to mention that the abundance of predators, per example, might also influence the growth bars as one constrain the passerines to look for food.

Secondly we would like to check which factors related to our study population are affected by the territory/individual quality and stress levels. In order to complete this aim, we suggested 3 different variables:

1) Flock size;

Once that ptilochronology measurements are a proxy for individual/environmental quality, we expect the flock size to be higher as lower the individual/environmental quality is. This effect might be present once that flocks in worst habitats will need more helpers to achieve in the end the same reproductive success.

2) Pulli weight;

We predict that there will be no differences between pulli weight and BF/environmental quality. We think that helpers in certain flocks will compensate for bad BF/environment quality and therefore camouflage the negative impact that it might have.

3) Fledging date;

Although very few studies were conducted in tropical habitats relating these 2 variables, we do not expect any significant result due to little or no variance observed in the environment during the breeding season.

Thirdly, we expect to give an overview of the survival rate of juveniles from the moment that they fledge until independence (50 days after fledging). Through this, we will be able to assess whether there are different survival rates among fragment as well as among the study period. It will be possible by then to confirm which one it is the critical moment where fledglings are more predisposed to decease. We expect the first weeks to be the critical period for juveniles, resulting in low survival rates. The subsequent weeks are instead expected to be less critical and thus result in higher interval survival rates.

Ultimately we want to identify the main factors that are related with survival rate. This will allows to understand how these factors affect survival from fledging onwards and in addition give insight in how the influence of these factors on survival rate changes temporally. With this purpose, we selected 4 different explainatory variables:

1) Flock size;

We expect flock size to be positively correlated with PFS. The *many-eyes hypothesis* (p.e.) explains that bigger groups imply more vigilance, so faster predator detection and more time for the pulli to disperse what leads to a higher REFS;

2) Pulli weight;

Many studies in temperate regions found a positive relationship between pulli weight and its survival probability. Although, once our study site is tropical, we should be careful when point out an expected result. Predation rate is known to be very high in this type of habitats. Due to the pulli fragility during the first days, such fact my influence the PFS independently of its weight.

3) Different fragments;

Aerts *et al.* (2010) showed that indigenous forest fragments vary in vegetation communities what might indicate different fragments quality, leading to different PFS values. Although, very little information exists about food availability, human disturbance and the amount of predators in each fragment, making it difficult to predict any result.

4) Fledging date;

Similar studies conducted in temperate regions showed strong correlations between fledging date and PFS with early fledge birds having higher survival rate compared to late fledge individuals. Although, once that we perform our study in a tropical habitat, we expect no relationship between fledging date and PFS because of the constant food availability in this type of environment.

Ultimately, such knowledge might enlighten us about Cabanis's Greenbul population dynamics and possible about the origin of such unique behaviour as the cooperative breeding.

Materials and Methods

Study Area

The Taita Hills (3°25' S, 38°20' E) represent the northernmost region of the Eastern Arc Mountains (EAM), a chain of mountains running from Southeast Kenya to the South of Tanzania. The EAM is often referred to as a global biodiversity hotspot [15] and a priority Important Bird Area (International, 2015). Bird endemism in this area is high, with both endemic and near-endemic species (Burgess, 2015). With an estimated area of 35.000 ha, it is located in the Taita – Taveta district and rises from the semi-arid plains of Tsavo (600m a.s.l.) (Naef-Daenzer, 2005; Aerts, Thijs et al., 2010; Spanhove, Callens et al., 2013; Vangestel, Callens et al., 2013; International, 2015). These plains separate the Taita Hills from other highland regions over a 50km radius (Spanhove, Callens et al., 2013; International, 2015).

The region can be divided into three main massifs (fig.1). Dabida, where our study was conducted, includes the high picks of Ngangao (1956m) and Vuria (2228m). Here is located Wundanyi town, the administrative centre of Taita-Taveta County and comprises a population of

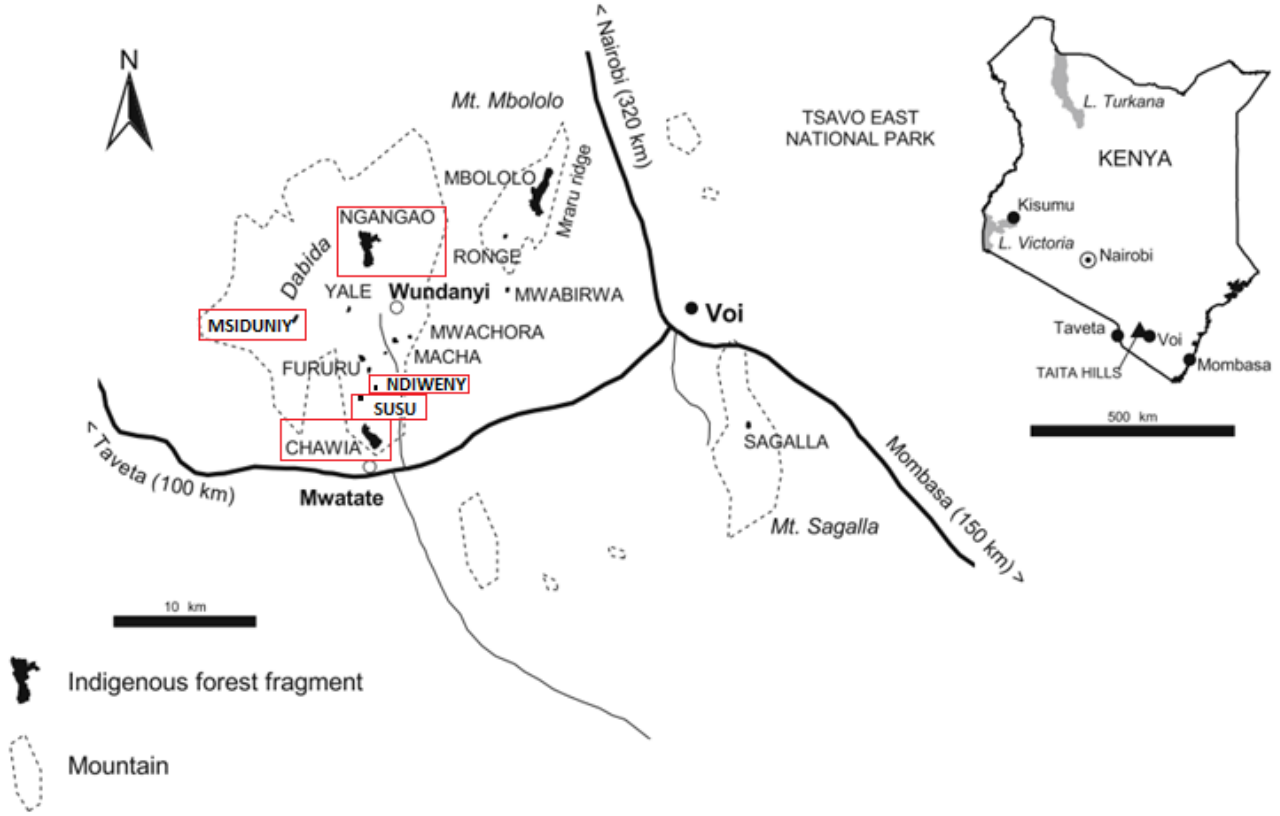

Fig. 1 Map of Taita Hills. Adapted from Aerts,R., et al.2010.

4055 habitants (1999 census). Sagalla, the most southern area, is separated from the rest of the Hills by the Voi River. Lastly, Mbololo, in the extreme northeast, which includes the biggest indigenous forest fragment of the region [4].

The Indian Ocean strongly affects Taita Hills. Its ridges and hilltops form a natural barrier to the south eastern winds generating two rainy seasons, one occurring during March-May and a shorter one during November-December (Pellikka P., 2004; Thijs, Aerts et al., 2014). The influence of the Indian Ocean also plays an important role in explaining the high level of endemism in this ecoregion (Githiru, Lens et al., 2011). The constant temperature and rainfall occurring on that water mass during the last 30 million years, leads us to believe that the Ice Age period was less extreme on the land mass surrounding the Indian Ocean, compared to the rest of the world. This might have been enough to allow the survival of the forests of the Eastern Arc Mountains and therefore explain the great biodiversity present today (Prell, 1980; Lovett, 1993). Taita Hills in particular, is consider to be a biodiversity hotspot (Myers, 2000), due to its outstanding diversity of flora and fauna and

very high level of endemism among vertebrates, invertebrates and plants (Pellikka, Lötjönen et al., 2009). Furthermore, this region is home to three endemic bird species as well as a considerable number of other threatened bird species (International, 2015).

Despite its ecological importance, this area has been suffering intense human pressure mainly due to the high fertility of the soil and good climatic conditions (Pellikka, Lötjönen et al., 2009). Therefore, forest remains as sole scattered fragments on the hilltops and ridges (International, 2015).

Taita Hills' cloud forest currently covers an area of 430 ha, reflecting 98% forest reduction over the last 200 years. This cutback is mainly due to clearance for timber and agriculture (Githiru, Lens et al., 2011), often followed by the plantation of exotic species due to its fast-growing and farming-friendly characteristics (Githiru, Lens et al., 2011; International, 2015). The effect of replacement of indigenous forest by exotic plantations has been deeply studied during the last years, including in tropical areas as Taita Hills (Beentje, 1988; Wilder, Brooks et al., 1998). In general, exotic forests do not provide adequate breeding, foraging or recruitment habitat for forest-restricted animal species, like the Cabanis's Greenbul (*Phyllastrephus cabanisi)* (Pellikka, Lötjönen et al., 2009; Loock, 2012). Therefore, this might lead to high levels of stress that generate a negative effect on the population (Lens, 1999).

Nowadays, there are twelve indigenous forest remnants, ranging between 1 ha and 180 ha and all situated above 1350m (Githiru, Lens et al., 2011). Our study was conducted in five of these forest fragments: Chawia, Msiduniy, Ndiwenyi, Ngangao and Susu.

Ngangao (38˚20´33''E, 3˚21´55´´S) is the biggest forest fragment of the Dabida massif with a total area of 120 ha (Aerts, Thijs et al., 2010) reaching an altitude of 1,952m at its highest point (Wagura, 2014). The indigenous forest is located 4.5km northwest of Wundanyi on the steep eastern side of the hill, while plantation and rock outcrop occupy the western side. During the last 50 years, this fragment has suffered a reduction of 50% in indigenous forest (International, 2015) although presently no more logging occurs (Loock, 2012). This area is especially important once it is a hotspot of Taita's endemic species (Wagura, 2014).

Chawia (38˚20'31''E, 3˚28'48''S) is the third biggest forest fragment in Taita Hills with an area of approximately 86ha (Pellikka PKE, 2009; Aerts, Thijs et al., 2010). The forest is located at the top of a cliff and has gentle slopes between 1470m and 1600m (Aerts, Thijs et al., 2010). Since the 1960's, forest loss has been substantial with estimates of 85% for this patch (International, 2015).

The last couple of years the local community has been restoring the forest by planting native tree species, trying to prevent the loss of endemic bird species (Wagura, 2014).

Susu (38°19'57.91"E, 3°26'55.80"S) is located roughly at 6km from Wundanyi and although it comprises 14.3ha of forest (Githiru, Lens et al., 2011), very little or no information is available. It comprises a mosaic of highly disturbed indigenous patches with exotics and small agricultural fields in between, therefore it is by most considered to be non-indigenous woodland.

Msiduniy (38°17'57.35"E, 3°24'13.99"S), located 7km west of Wundanyi town, was until recently, considered as part of the Vuria forest fragment. This area has been suffering intense deforestation resulting in only 1% remain of the original indigenous forest (2ha) (Githiru and Lens, 2004; International, 2015).

Ndiwenyi (38°20'35.20"E, 3°26'25.11"S) consists of a forest patch of approximately 4ha ranging between 1582 and 1605 meters of altitude (Githiru, Lens et al., 2005).

Study species

Cabanis's Greenbul, *Phyllastrephus cabanisi* (Sharpe, 1882)(fig.2) is a medium-sized, brownish passerine, classified within the Pycnonotidae family (Fishpool). It is found over part of Central Africa in countries such as Angola, Democratic Republic of the Congo, Mozambique and Kenya, inhabiting primary and secondary forests, as well as woodland of various types up to 2700m of altitude (Del Hoyo and Cuckoo-shrikes to thrushes. Lynx Edicions; Brooks, Lens et al., 1998). Although it has been observed or trapped in all the twelve forest fragments of Taita Hills, breeding is restricted to only a few of them. Even though this species has quite a large range, recently it has been shown that Taita Hills meta-population comprises a closed network that is strongly isolated from the nearest *P. cabanisi* populations in the Chyulu Hills (Kenya, ca. 100 km NW) and Pare Mountains (Tanzania, ca. 100 km SW) (Husemann, Cousseau et al., 2015). Recent demographic and genetic studies in Taita Hills show that Cabanis's Greenbul population has at the moment an overall trend of increasing population size (Husemann, Cousseau et al., 2015). Globally, this species is considered to have a wide range distribution and stable population trend and therefore is listed as "Least Concern" (International, 2015). Cabanis's Greenbul is considered to be a facultative cooperative breeder and is often seen foraging in pares or in small family groups (breeding pair and 0–3 helpers, Van de Loock, unpubl. data) (Vangestel, Callens et al., 2013; Husemann, Cousseau et al., 2015). Although it is considered to be an insectivore, Cabanis's Greenbul occasionally feeds on

fruits, but supplies nestlings with invertebrates and more rarely with small vertebrates (Aben, Adriaensen et al., 2012; Husemann, Cousseau et al., 2015).

In this species both male and female are responsible for building cup-shaped nests at an average height of 1.3m in shrub, climbers or small tree species such as *Chassalia discolor*, *Culcasia scandens*, *Dracaena steudneri* and *Uvaria* sp. (Loock, 2012; Spanhove, Callens et al., 2013). The breeding season occurs from mid-October to mid-March. Most clutches contain two eggs with very rare exceptions of three eggs (Callens, 2012; Spanhove, Callens et al., 2013), being incubated for 17 days, by the female. Nestlings fledge after approximately 11-13 days (Callens, 2012).

Fig. 2: Trapped adult Cabanis's Greenbul (Phyllastrephus cabanisi). Photo by Alexandre

Data collection

Data collection and methodology

During the last 19 years, intensive ringing has been carried out in the indigenous forest fragments of Taita Hills. Nowadays at least 75% of *P. cabanisi* are marked with an aluminium ring in combination with three colour ring creating a unique colour combination that allow us to identify each particular individual in the field. Between November of 2014 and March of 2015, four field assistants surveyed all the indigenous forest fragments of Dabida massif trying to locate Cabanis's Greenbul nests. Once an active nest was found, its latitude and longitude were registered and were revisited every four to six days to assess its outcome (predated in egg or pulli phase or successfully fledged).

Dries van de Loock executed a pilot study where he placed transmitters in the pulli in order to follow them and ascertain their biological fate. This pilot study not only revealed that placement of transmitters in Cabanis's greenbul pulli is highly unsuccessful, but also revealed that juveniles remain very close to the BF during the dependency period. These preliminary results led us to place

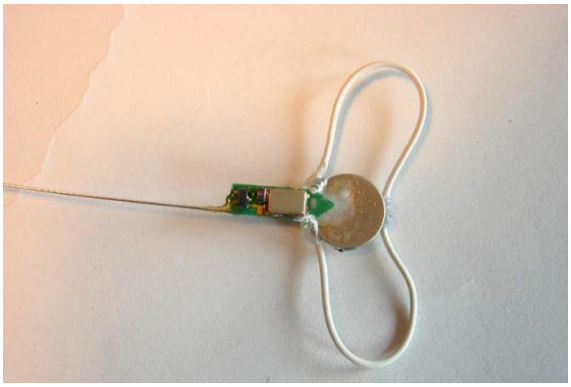

Fig.3: Rubber threads in loop shape attached to the transmitter. Adapted from (Rappole, 1990; Naef-Daenzer, 2005; Naef-Daenzer, 2007)

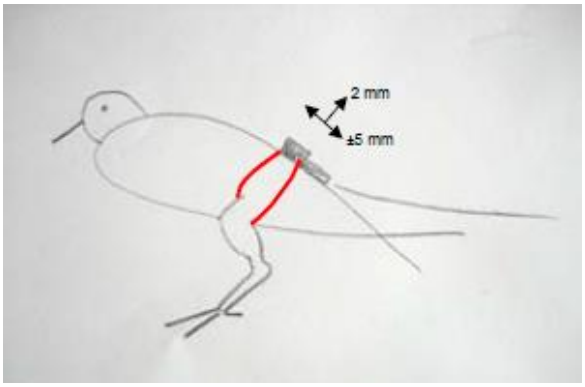

Fig. 4. Correct attachment of the transmitter in the bird using the leg loop technique. Adapted from (Rappole, 1990; Naef-Daenzer, 2005; Naef-Daenzer, 2007)

the transmitters in the BF and use them to locate and sight the juveniles. The transmitter was placed on the BF after the hatch of the pulli and was attached using the leg-loop technique. This consists of two natural rubber threads in loops connected with the transmitter that are slipped over each leg of the bird (fig. 3). In the end, the transmitter should be positioned between the rump and the mantle creating a sort of a 'backpack' that the bird is able to carry around, interfering as little as possible on its normal activity (fig.4) (Rappole, 1990; Naef-Daenzer, 2005; Naef-Daenzer, 2007).

The following question rises then: "Why had the allocation of transmitters such a negative impact in the juveniles?" The answer to this question is based on the physical fragility of the

juveniles. Due to the low development of the flight and the lower weight of the juvenile (the transmitter therefore represents a higher percentage of the total body weight, what will lead to a greater use of energy by carrying the transmitter), it is less disturbing to allocate the transmitter on the BF. Furthermore, a lot of transmitters are lost due to presumed early predation events or failure of solid attachment. The tracking was mainly focused on the breeding females (BF) in which the offspring survived until they fledge. Although, we also tracked breeding females that suffer nest predation in order to access the re-nesting period. For this exercise, two short-length mist nets were positioned perpendicularly around the nest and birds were lured with a distress call maximizing the efficiency of the nets (Gregory, Gibbons et al., 2004). The playback lure was active for a maximum of 10 minutes with a continuous loop of alarm calls located 1m from the nest.

Due to the high disturbance impact and to the fragility of the pulli within the first six days, we divided the ringing of the BF and nestlings in two different sessions. The first, when the pulli were around six days old, and a second one, at ten days old. In both sessions, the individuals were metal ringed and colour banded, measured and physiological samples were collected.

Standard morphometric measures were recorded (wing-, bill-, head- and tarsus-length; weight) and both second outer tail feathers and body feathers were collected. In addition, a capillary of blood was collect from the brachial vein from the breeding females (BF) for future genetic work. Individuals were released as soon as possible in the same spot where the capture occurred. No nest was disturbed more than 1 hour per session.

Individuals caught and/or observed close to the nest with clear affinity for that nest were considered associated individuals. When more than two members were associated with a nest, the flock was considered cooperative. However, if only a female and male were seen at the nest, the flock was considered to be a non-cooperative and both individuals were considered to be the breeding pair. Breeding females were identified based on breeding patch (as only one individual caught had a breeding patch[1]), as well as on the amount of nest care dedicated to the nest (i.e. the longest time incubation was considered to be the breeding female).

---

[1] *One or more areas of the ventral surface where the skin is thickened and richly supplied with blood vessels. This adaptation facilitates the transfer of heat from the body of the incubating bird to the eggs. In Passeriformes only the females show this patch* Bailey, R. E. (1952). "The Incubation Patch of Passerine Birds." The Condor 54(3): 121-136..

Relocating BF and juvenile after fledging

To relocate the BF a Biotrack flexible 3-element Yagi antenna with a Sika receiver synchronized at a 152 MHz was used. This system is based on radio waves with a specific frequency. Each frequency is associated with a unique transmitter and therefore with a single individual. The receiver allows to select a specific frequency to look for and, as soon as the antenna receives it, it emits a short and loud 'bip' sound each 2 seconds. The tone of the 'bip' varies according to the proximity of the individual to the antenna.

The studied breeding females were located each 5^{th} or 6^{th} day for a minimum of 9 times.

The tracking session initiate after occurrence of one of the two following situations:

1 - One or more individuals were seen or heard accompanied with a strong enough signal at the same time and from the same direction;

2 – The signal of the transmitter was very strong and suddenly dropped and became very weak (even if the bird is not seen or heard). This means that the individual was close (due to the strong signal) but disperses away from the receiver (the reason why the signal weakened). The flock was followed until all the fledglings and BF were found or until 45 minutes after the tracking started.

For each tracking session, a value of mobility and defence is attributed to the flock as well as a value for the defence level of each observed individual. This allowed to infer which were the most active individuals concerning the defence of the flock and therefore conclusions could be made about the role of each one of them inside the flock. We also assessed the flock composition by writing down all the colour ring combinations observed in each session. Flock size was difficult to access in the field due to the bird's fast movements and dense vegetation. Thus, in order to incorporate that uncertainty, we chose to use a minimum and a maximum flock size number. *Special behaviours* from any bird in the flock were noted down. Such behaviours can include high and constant alarm calls, crawling on the floor with spread wings or jumping from branch to branch fast and energetically. After some field work studying Cabanis's Greenbul, we realized that these behaviours are a response to disturbance and only happen when pulli are still alive. This allows us to make more accurate estimates about the presence/absence of the fledglings.

Ptilochronology and Fluctuating Asymmetry

Our ptilochronology measurements were obtained by positioning each feather on a white paper and using a digital slide caliper (up to 0.01mm). After, the central growth bar was identified and marked. For this purpose, we calculate the '7/10th point' (the point at a distance of 7/10 of the total feather length, starting from the proximal end of the feather). A growth bar consists of a proximal 'light band' and a distal 'dark band' perpendicular to the rachis of the feather (Grubb, 2006). From the central growth bar, two additional proximal and two additional distal growth bars were marked using a ultrafine mounting pins (0.27mm diameter) together with a headband magnifier with x2.5 magnification (more details in (Frasz, Fischer et al., 2013)) . If the '7/10th point' fell within a 'light part' of a growth bar, this growth bar became the central growth bar and two additional proximal and two additional distal growth bars were measured (Fig. 5). If the '7/10th point' fell within a 'dark part' of a growth bar, the next distal growth bar became the central growth bar (Fig. 6). Each marked paper was then scanned and growth bar sizes were automatically measured with image analysis software (KS400 Zeiss).

In order to have a more accurate data set, each feather from the same BF was measure at least two times (sequence left-right-left-right or right-left-right-left) and all measurements were performed by A.R. and always under the same equipment and laboratory circumstances.

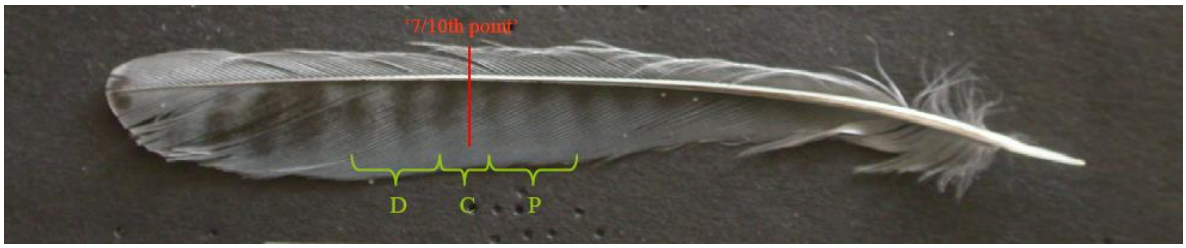

Fig. 3.: Situation where the 7/10th point falls within a "light part". C = central growth bar, P = 2 additional proximal growth bars, D = 2 additional distal growth bars. Adapted from (Vangestel, 2006)

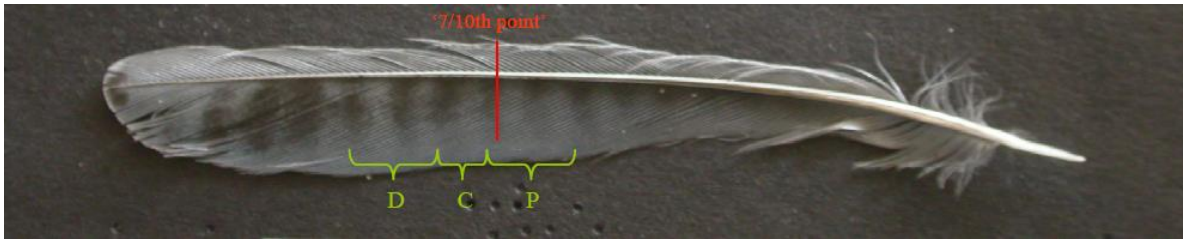

Fig. 6.: Situation where the 7/10th point falls within a "dark part". C = central growth bar, P = 2 additional proximal growth bars, D = 2 additional distal growth bars. Adapted from (Vangestel, 2006)

Fluctuating asymmetry was calculated by comparing the difference in length between left and right second outer tail feathers (Lens, 1999). Since levels of asymmetry can be really small (on average 1-2 % of the total trait size) and measurement errors (ME) can be high, true levels of asymmetry can be overestimated or be masked relatively easily. To overcome this problem, both left and right feathers were measured twice alternatingly (Knierim, Van Dongen et al., 2007).

We observed high repeatability among feathers measurements from both sides (Right side = 0.9836398, $p < 0.0001$; Left side = 0.9953459, $p < 0.0001$). For this test we used Person's correlations.

Despite our high repeatability, an average of the ME should have been incorporated in our mixed model in order to eliminate its influence on our results (Lens, 1999). Due to logistic difficulties this procedure was not applied here.

Once that there are 3 different possible types of biological asymmetry, it was necessary to test which one of them our data fits the best. By studying the statistical distribution of difference between left and right measurements (Shapiro-Wilk normality test: W = 0.93057, $p = 0.1583$) we were able to tell that our data reflects a fluctuating asymmetry, rather than directional asymmetry or antisymmetry. Once fluctuating asymmetry has been established to exist in our trait, we proceed by testing for the relation between trait size and the respective FA. Once that there was a strong relationship (linear model: $p = 0.00169$), this trait was also added to the model as a fixed effect.

In order to be able to compare FA values and the continuous variables it was necessary to use the absolute FA values, sometimes called *unsigned* values (Kotiaho, 2001).

Statistical analyses

In general, my results are based on the information captured from 35 pulli from 21 different nests. Once that 2 BF renested the number of BF is then 19. All the BF used in this study had a radio-transmitter attached that we used to get to the pulli.

Body condition and individual development

As a proxy for body condition of fledglings, we used the residual values of body weight over tarsus length (which is a good indicator for bird size (Jackson, 1990; Green, 2001)). As a proxy for development we used the residuals of wing length over tarsus length. This relative scale indicates if individuals have developed their feathers more than expected based on their size. Individuals with

positive values would thus be able to fly faster and be less prone to predators. We incorporated age at time of measuring in the regression as when calculating the residuals in both models to correct for age-related differences in weight and feather development.

Ptilochronology

There are two basic approaches to conceptualizing how to measure habitat quality is normally measured based on two different approaches: either directly by measuring attributes of a habitat itself, or either indirectly by measuring variables of individuals and/or populations in different habitats to reveal variations in habitat quality (Morrison, Marcot et al., 2012). When measuring habitat quality directly, we should of course be concerned with critical resources, such as food and nest sites. Although is equally important to account for ecological constraints that may limit the use of those resources, such as risk of predation, intensity of competition, and physical accessibility of resources. Habitat quality is therefore defined not only by the resources necessary for survival and reproduction, but also by the conditions that constrain their use (Johnson, 2007). On our study, the direct approach was not available due to the lack of data concerning our study territories. Thus, we used an individual-based indirect method, ptilochronology. We will use the bar width (BW) of the left and right tail feather from each breeding female as a proxy for habitat quality.

Each measurement is based on the average BW of the repeated measures for each feather and then averaged these between left and right feather.

In the ptilochronology analyses, nest was removed from the random effects once that only one value of BW is assigned per nest.

Average tail feather length was always added as a fixed effect during this set of analyses once that BW had a strong relationship with this trait. On the contrary, BW was not correlated with BF body weight (*Estimation* = 0.17442; *Std. deviation* = 0.20763; *df* = 16.77100; *t* = 0.840; *p* = 0.413) or average tarsus length (*Estimation* = -0.1482; *Std. deviation* = 0.1091; *df* = 17.0570; *t* = -1.359; *p* = 0.192) therefore these variables were not added in the model.

Fragment was analysed through GLM and average tail length was *scaled* due to very large eigenvalue. *Scale* is a generic function whose default method centers the columns of a numeric matrix. In other words*,* subtract the mean of all data points from each individual data point. In order to test each fragment against each other, we applied a Tukey-Post Hoc test to our model.

We tested whether flock size was significantly correlated with BW of the female. We used a GLMM with *scaled* average tail length as fixed effect and fragment as random effect.

The same methodology was used to test the influence of habitat/individual quality on cooperation, body condition and individual development from both BF and pulli and fledgling date.

Fluctuating asymmetry

FA is a measure dependent on the average tail feather length (TL). Two birds exposed to the same level of environmental stress will show different FA level if both have different feather's size. Therefore we added scaled TL as a fixed effect in all the model here described.

As before, this variable was tested against the previously mentioned factors (i.e. fragment, flock size, cooperation, BF and pulli body condition, BF and pulli individual development, fledgling date and habitat/individual quality).

During this series of analyses, we used GLMM with Gaussian family and log link function as well as fragment as a random effects. Exception was made for the FA vs Fragment model once that there were no random effect associated and therefore a simple linear model was enough. Moreover, in order to test each fragment against each other, we applied a Tukey-Post Hoc test to our model.

For the statistical analysis of body condition and individual development for both breeding female and pulli, we used fragment as a random effect. Nest was not used as a random effect once that there was only one value of FA per nest. The same happened for flock size, fledgling date, BW, and cooperation.

Post-fledgling survival

All the nests that had the BF with a transmitter and in which at least one pullus fledged succesfully (N=21) were included. Due to the fact that some females renested, our number of BF differs from the number of nests.

After each tracking session we concluded that the fledglings were alive when visually observed or when the behaviour of the flock indicated its presence by showing some specific behaviours. All the analysis were performed in R (version 3.2.2).

During the statistical analyses, we understood how complex it is to use 2 values to express the flock size (minimum and maximum). Therefore, we checked first how both values correlate with each other. Once that there was a strong positive correlation ($p < 0.001$), we decided to use only the maximum number of individuals present in the flock.

In order to accommodate for temporal variation in survival, we assessed to relation of survival with our variables of interest (see below) on two temporal intervals. The first model-set deals with the survival from fledging until day 5, the second model-set from day 5 until day 20. We divided these temporal intervals arbitrary, based on an abrupt decline in survival from day 0 to day 5 and a relatively stable stable survival between day 5 onwards. This suggest that survival of juveniles is influenced at different scales or by different variables at various age-class stages after fledging.

For both model-sets, we modelled survival (discrete variable) as a dependent variable and fragment, flock size, cooperation, body condition of the BF and pulli, individual development of BF and pulli, pulli fledgling date, habitat/individual quality and environmental stress levels as independent variables. For each variable, two tests were conducted, corresponding to the 2 analysed periods. During this stage, in all models logit-link function was used. This function is simply the mean of the response variable X and we use it as the response instead of X itself (ALLISON, 1999).

Fragment was tested by using a generalized linear model (GLM) and nest was only added as a random effect in the period before 5 days once that the model did not converge in the other remaining period. In order to test each fragment against each other, we applied a Tukey-Post Hoc test to our model.

Flock size was then analysed by using generalized linear mixed model (GLMM) (flock size against post-fledgling survival before 5 days and after 5 days). For these tests nest and fragment were used as random effects.

Our variable *cooperation* was integrated in order to answer the specific question if the presence of helpers (independently of their number) would have any correlation with post-fledgling survival. Therefore, *cooperation* was admitted as a binomial variable with fragment and nest as random effects, using a generalized linear mixed model (GLMM).

Body condition and individual development of the pulli and BF were tested as well in order to understand if the physical state of the pulli and of the BF had any significant influence in the post-fledgling survival of the pulli. This was achieved by using as well a GLMM with fragment and

nest as random effects. Particularly for the pulli body condition and development, pulli age upon measurement was added as a fixed effect once that individuals with different age will have different weights and wing sizes.

In order to check the relative importance of the fledgling date in the post-fledgling survival of the pulli, and therefore understand the possible relationships among both variables, we used a GLMM with fragment as random effect. Nest should have been added although the model did not converge so therefore was removed. We defined fledgling date as day 0 for survival history.

Extra tests were performed in order to check whether or not there are extra significant correlations that might therefore influence the results we are actually interested on. By using a GLZ, we checked for instance if there is or not a difference on the amount of cooperative behaviour incidence among fragments. As previously mentioned, our studied population is thought to have a load-lightening strategy (Callens, 2012). It was therefore intuitive to model as well flock size against pulli weight and BF weight. If this behaviour is indeed adopted by Cabanis's Greenbul in Taita hills, we would expect a positive correlation between BF weights and flock size and no correlation between flock size and pulli weight. For both analyses we used a linear mixed model with fragment as a random effect, although for pulli weight against flock size we add age as a fixed and nest as a random effect.

Bar width was modelled against post-fledgling survival (PFS). For this analyses, we used a GLMM with fragment and nest as random effects and scaled total tail feather length as a fixed effect. Once the dataset was composed of zeros and ones, we used binomial family together with logit-link function. Once that we subdivided our PFS data in 2 different moments (before and after 5 days) we also had to have 2 different moments relating PFS and BW, one before and one after the 5^{th} day.

Ultimately, post-fledgling survival was also tested against FA. In the first moment, the full data set was used and in the second one, only the individuals that had survived until the 5^{th} day were considered (same as in the ptilochronology analysis). In both moments, we perform a GLMM with fragment and nest as random effects.

For both model sets, we ran univariate generalized linear mixed model with survival as dependent variable and fragment, flock size, cooperation, body condition of the BF and pulli, individual development of BF and pulli, pulli fledgling date, habitat/individual quality and environmental stress levels as independent variables. We added nest, nested within fragment as a random factor with all models except when modelling the direct effect of fragment on survival.

When models did not converge due to small sample sizes, we omitted the random effects and ran univariate generalized linear models instead. When the independent variables were composed of values originated directly from the pulli, age upon measurement was added as a fixed effect.

Results

Ptilochronology

Growth bar width does not change significantly between fragments (table 3). Individual/habitat quality did not show to be highly different among each of the studied sites.

Table 1: Tukey-Post Hoc test relating growth bar width among fragments;

Fragments	Estimate	Std. Error	t value	p value
MS - CH == 0	-1.20996	0.83798	-1.444	0.600
ND - CH == 0	-0.72074	1.28140	-0.562	0.977
NG - CH == 0	-0.79941	0.71540	-1.117	0.787
SU - CH == 0	0.04288	0.83265	0.051	1.000
ND - MS == 0	0.48922	1.36039	0.360	0.996
NG - MS == 0	0.41055	0.82922	0.495	0.986
SU - MS == 0	1.25283	0.96926	1.293	0.689
NG - ND == 0	-0.07867	1.25933	-0.062	1.000
SU - ND == 0	0.76361	1.37216	0.557	0.978
SU - NG == 0	0.84228	0.87299	0.965	0.861

We also tested the possible influence of growth bar width in the maximum number of individuals in one flock. There was no significant ratio among these 2 traits, although it was clear that the regression had negative signal (*Estimation* = -0.443896; *Std. deviation* = 0.262132; *df* = 18.000000; *t* = -1.693; *p* = 0.1076), meaning that as bigger the growth bar width, as smaller is the flock.

Cooperative behaviour decreases as the BF growth bars increases, although this relationship was not proven to be significant (*Estimation* = 0.4945; *Std. deviation* = 0.4576; *t* = -1.081; *p* = 0.280)(fig. 7).

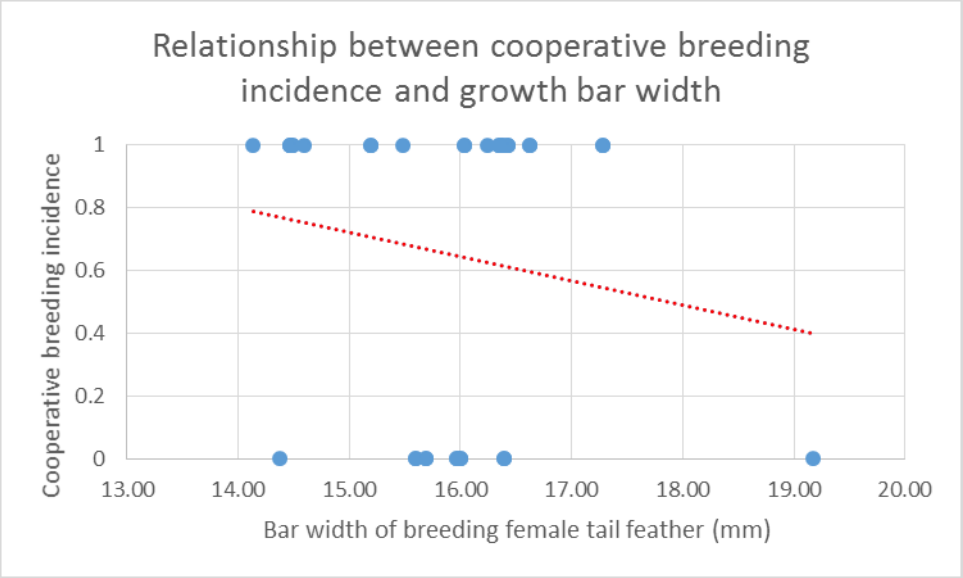

Fig. 7: Negative correlation between individual/habitat quality and the cooperative breeding incidence;

Despite the weight residuals (body condition) of the BF represent partially similar information as the width of the growth bars (ptilochronology), we thought it could be interesting to test them against each other once that both measures are relative to different life periods of the individual. This trait showed no significant relationship between the BW *(Estimation* = 0.2466; *Std. deviation* = 0.1868 *df* = 16.8280; *t* = 1.320; p = 0.205) while fairly to the individual development a strong positive correlation was found (GLMM: *Estimation* = 0.3990; *Std. deviation* = 0.1787; *df* = 19.0000; *t* = 2.232; *p* = 0.0378). Relatively to the juveniles, this trait, as well as body development did not show any significant result (all tests: $p > 0.1$)

Fledgling date was also not influenced by the ptilochronology results (*Estimation* = -0.14621; *Std. deviation* = 0.15309; *t* = -0.955; *p* = 0.3395). Individual quality/habitat quality does not plays a role upon the reproduction date and therefore the fledgling date.

Fluctuating asymmetry

When analysed through the linear model, Ngangao showed a significant difference in FA (*t* = -2.352; *p* = 0.03381) when compared against Chawia. This result was although not confirmed when observed through Tukey-Post Hoc test, showing that the correlation previously observed was not

sufficiently strong. All the others did not show any strong relationship both in the linear model and in the Tukey-Post Hoc test (table 4).

Table 2: Tukey-Post Hoc test relating fluctuating asymmetry among fragments;

Fragments	Estim.	Std. Error	t value	p value
MS - CH == 0	-0.8942	0.7466	-1.198	0.744
ND - CH == 0	-2.3691	1.1421	-2.074	0.274
NG - CH == 0	-1.4964	0.6361	-2.352	0.178
SU - CH == 0	-0.4780	0.7405	-0.645	0.963
ND - MS == 0	-1.4749	1.2100	-1.219	0.732
NG - MS == 0	-0.6022	0.7389	-0.815	0.918
SU - MS == 0	0.4162	0.8640	0.482	0.987
NG - ND == 0	0.8727	1.1225	0.777	0.930
SU - ND == 0	1.8911	1.2235	1.546	0.541
SU - NG == 0	1.0184	0.7764	1.312	0.678

Continuing in our analyses, FA showed not to have a significant impact in the maximum number of individual in one flock (t = 1.106). Although it is important to notice that the observed relationship has a positive signal, meaning that high/low values of FA leads to big/small flocks respectively.

Cooperative breeding incidence was modelled against our trait and no significance correlation was observed, although the regression signal was positive (z = 1.477; p = 0.140). This indicates that, even not significantly, each bird performs cooperative breeding behaviour upon higher environmental stress levels.

Like ptilochronology, FA was also tested against body condition and individual development of both the BF and PU. For any of them it was observed a significant correlation (all tests: $p > 0.1$)

Fledgling date showed not to be influenced by the FA (p = 0.1410). As it happened with ptilochronology, birds are not significantly dependent in FA when it comes to reproduce in a particular day and therefore to have a specific fledgling day for the pulli.

At last, no relationship was found between FA and ptilochronology values (Estimation = 0.005601; *Std. deviation* = 0.014226; t = 0.39; p = 0.694) indicating that probably different factor influence these two traits.

Post-fledgling survival

In total, 35 pulli from 21 nests were studied. During the 50 days that we followed each individual, the period where the biggest amount of pulli deceased was during the first 5 days after fledgling with 45.7% missed juveniles. Until day 20, an additional 14.3% of the individuals were never observed again. From day 20 to day 50 no pulli deceased (fig.8).

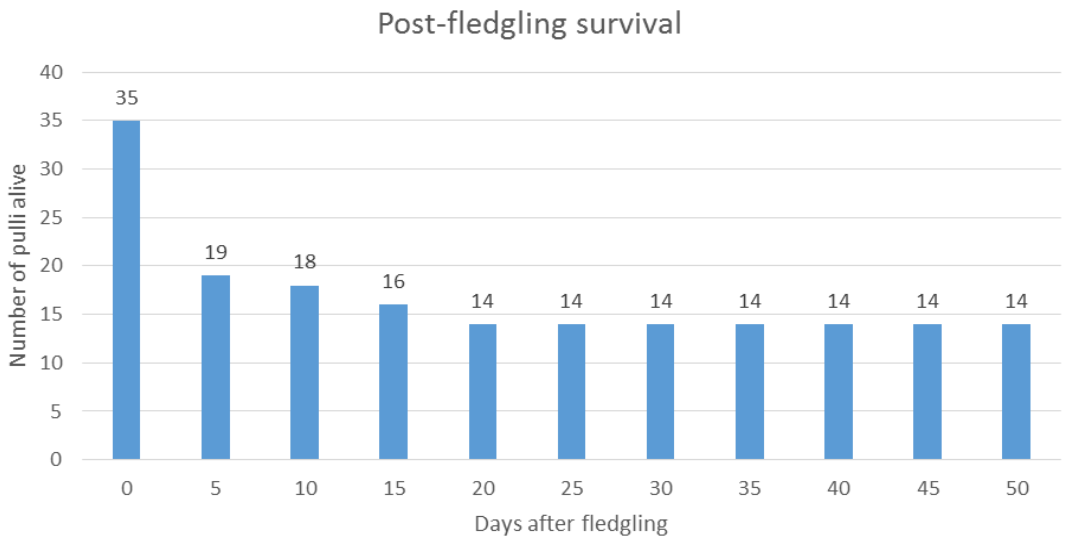

Fig. 8 Distribution of the number of pulli alive per each 5 days;

Ngangao (n=14) and Chawia (n=10) (fig. 9) are the two biggest fragments, representing together almost 68% of all the studied individuals. Despite the high initial number of fledged pulli in Ngangao, only 3 individuals survived until day 50 what comprises a survival of 21.4%. Msiduniy was the fragment where the survival rate was lower with 0 pulli alive after 50 days. Susu, on the other

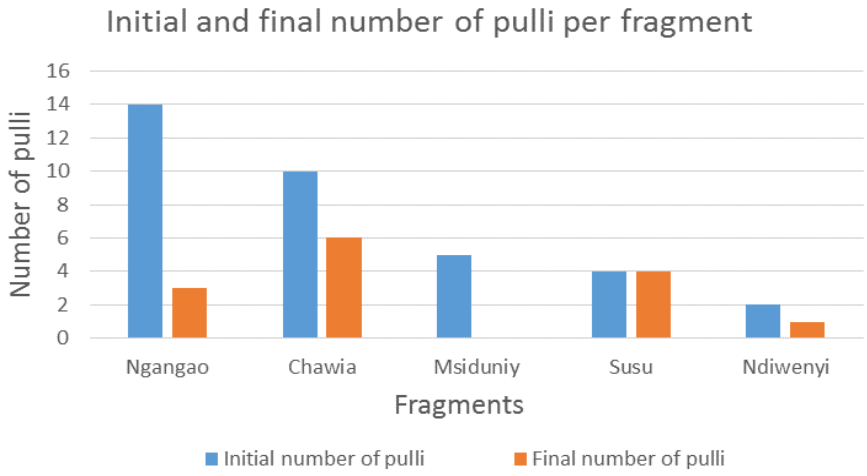

Fig. 9: Number of pulli at day 0 (fledge day) and at day 50 per fragment.

hand, had a survival rate of 100% with 4 in 4 individuals alive. Chawia and Ndiwenyi had respectively 40% and 50% of survived pulli (fig.9).

The statistical analyses showed no difference between fragments in post-fledgling survival rate, in the first analysed period (from 0 to 5 days) (table 1). Although, in the second period (form 5 to 50 days) (table 2) there was a significant difference between Chawia and Msiduniy as well as between Susu and Msiduniy.

Table 3: Tukey-Post Hoc test relating post-fledging survival among fragments until 5 days after fledge;

Fragments	Estim.	Std. Error	z value	p value
MS - CH == 0	-0.20295	0.28063	-0.723	0.948
ND - CH == 0	-0.09902	0.39852	-0.248	0.999
NG - CH == 0	-0.16994	0.21226	-0.801	0.926
SU - CH == 0	0.40098	0.30154	1.330	0.659
ND - MS == 0	0.10394	0.43019	0.242	0.999
NG - MS == 0	0.03301	0.26703	0.124	1.000
SU - MS == 0	0.60394	0.34231	1.764	0.380
NG - ND == 0	-0.07092	0.38906	-0.182	1.000
SU - ND == 0	0.50000	0.44411	1.126	0.783

SU - NG == 0	0.57092	0.28893	1.976	0.265

Table 4: Tukey-Post Hoc test relating post-fledging survival among fragments from 5 to 50 days after fledge;

Fragments	Estim.	Std. Error	t value	p value
MS - CH == 0	-1.000e+00	2.673e-01	-3.742	0.0148
ND - CH == 0	2.081e-17	3.536e-01	0.000	1.0000
NG - CH == 0	-5.000e-01	1.890e-01	-2.646	0.1085
SU - CH == 0	0.000e+00	2.113e-01	0.000	1.0000
ND - MS == 0	1.000e+00	4.009e-01	2.494	0.1403
NG - MS == 0	5.000e-01	2.673e-01	1.871	0.3624
SU - MS == 0	1.000e+00	2.835e-01	3.528	0.0219 *
NG - ND == 0	-5.000e-01	3.536e-01	-1.414	0.6162
SU - ND == 0	-2.081e-17	3.660e-01	0.000	1.0000
SU - NG == 0	5.000e-01	2.113e-01	2.366	0.1731

Cooperatively breeding flocks had a marginally significant higher survival rate than those which did not perform this behaviour (*Estimation* = 1.3218; *Std. deviation* = 0.7528; *t* = 1.756; *p* = 0.0791). Although this relationship was less strong during the last 45 days (*Estimation* = 7.012; *Std. deviation* = 7.008; *t* = 1.001; *p* = 0.3170), this result is a crucial step in order to try to understand the importance of this behaviour on this species.

Flock size showed to be an important parameter in order to explain post-fledgling survival. The maximum number of individuals in one flock showed to be significantly correlated (p = 0.0171) with the pulli survival rate during the first 5 days after fledging. Juveniles living in larger flocks had more chance of surviving the first 5 days. This relationship was even stronger when looked from day 5 to day 50 (*Estimation* = 16.132; *Std. deviation* = 4.975; t = 3.242; p = 0.00119) (fig. 10). Such result needs to be interpreted carefully once that the reasons behind it can be numerous, including

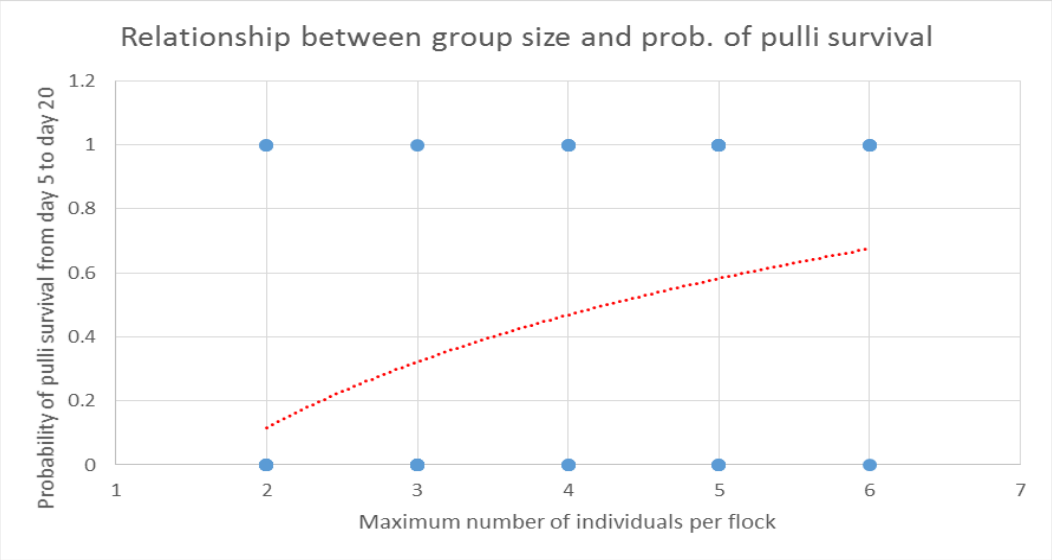

Fig. 10: Positive correlation between maximum flock size and probability of pulli survival from day 5 to day 20;

being a statistical fallacy.

Body condition and body development were not significantly related to post fledging survival in both time intervals (all p > 0.10) demonstrating that bird's condition and development state does not play a significantly important role on the survival of the juveniles.

Pulli survival was, as well, not significantly influenced by the fledgling date (*Estimation* = -0.008051; *Std. deviation* = 0 .018664; *t* = -0.431; *p* = 0.666) until day 5. Due to small sample size, the

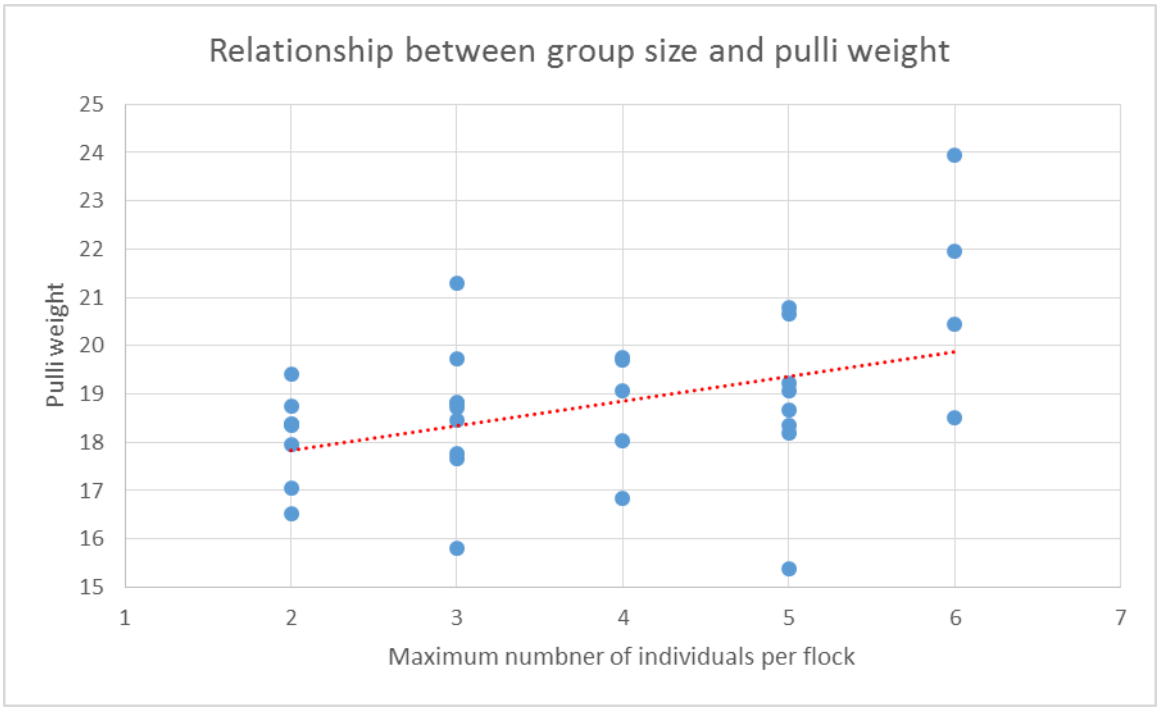

Fig.11: Positive correlation between maximum flock size and pulli weight.

model of the second time period did not converge.

There was no significant difference between fragments on incidence of cooperative behaviour on our studied species. On other words, this behaviour has approximately the same expression in all the studied fragments (Tukey-Post Hoc test*:* $F_{4/16}$ = 1.531*;* *p* = 0.2406).

Either pulli or BF body condition showed no relationship with flock size (Pulli GLMM: *Estimate* = 0.1679; *Std. deviation* = 0.1507; *df* = 12.6730; *t* = 1.114; *p* = 0.2860, BF GLMM: *Estimate* = 0.1283; *Std. deviation* = 0.1694; *df* = 16.8390; *t* = 0.757; *p* = 0.459)(fig.11). Pulli body condition increases with flock size, although not significantly.

Survival rate was not influenced by the growth bar width of the BF during the first 5 days (*Estimation* = -0.006342; *Std. error* = 0.453369; *z* = -0.014; *p* = 0.989). Although, the second period register a strong positive relationship (*Estimation* = 43.393; *Std. error* = 14.428; *z* = 3.007; *p* = 0.00263 < 0.01) (fig. 12).

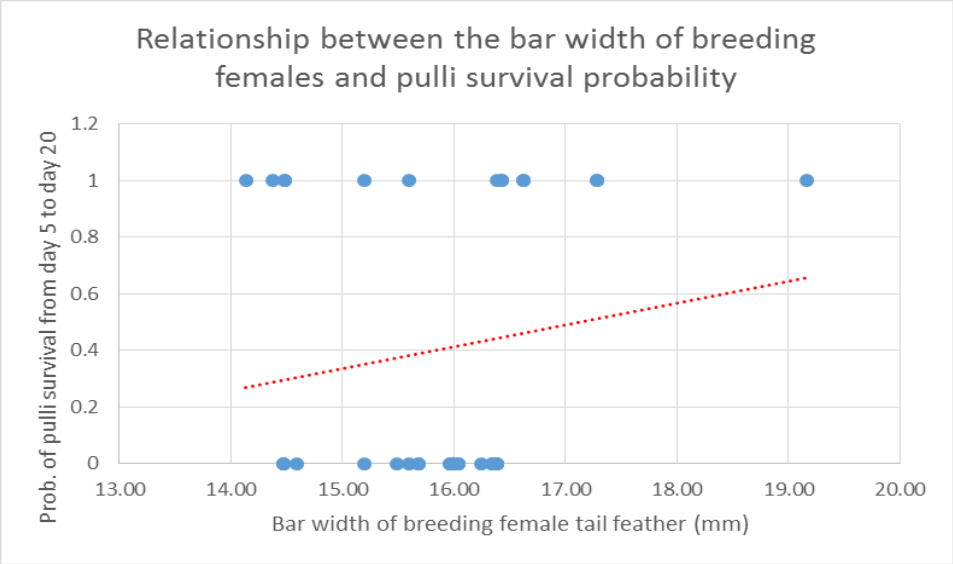

Fig.12: Positive relationship between breeding female bar width from the tail feathers and the probability of pulli survival from day 5 to day 20.

We tested as well the influence of FA over the observed post-fledgling survival before and after the 5th day. We verified a positive significant relationship, although only after the 5th day (*Estimation* = 34.681; *Std. deviation* = 12.872; *z* = 2.694; *p* = 0.00705).

Discussion

The incidence of cooperative breeding behaviour was not significantly different among fragments, what is in line with the finding of T. Callens (Callens, 2012), but in contrast with D. van de Loock work (Loock, 2012). The first author found that the percentage of nests aided by helpers did not differ between the two studied fragments but differed between the three years. My dataset was rather small due to the amount of workload that each next required, and it might be biased once that not all the found next were integrated in my analyses but only the ones with high relative importance for the project. Furthermore, D. van de Loock used a larger number of nests to perform the analysis, so I believe his results represent a more reliable perception of the reality.

Once that our studied species was associated with the load-lightening strategy (Callens, 2012), we were expecting helped breeding females to have a better body condition than the non-helped ones, although this relationship was not verified, at least significantly. Maede *et al.* (2010) points out that the marginal benefits of help for breeder survival are likely more difficult to identify than the increased productivity at helped nest (Meade, Nam et al., 2010). Besides, body weight of the BF was taken during nest phase. Here, the helper influence might still be low and therefore our results do not reflect the helper effect.

During our analyses, we verified the existence of, although not significantly, a negative correlation between the cooperative breeding (CB) incidence at our population and ptilochronology results. As explained before, low individual/habitat quality will generate reduced growth bar widths (low ptilochronology values). This means that CB might be an adaptive behaviour in order to compensate for low individual/habitat quality. If this is confirmed, only ind. with small growth bar width will perform it. Furthermore, this line of thinking will lead us to conclude that indeed no differences in the breeding females body condition should exist once that birds with high individual/habitat quality will not have helpers (no additional benefit), and birds with low individual/habitat quality will use helpers to save resources leading them to the same body condition status as non-helped females.

Pulli body condition was also non-significantly correlated with different flock sizes. As Tom Callens described in (Callens, 2012), helpers did not affect reproductive output once that aided female breeders reduced their feeding frequency, leading the overall feeding frequency remaining the same. Is therefore logical that no difference was found in the pulli body condition of big flock sizes (cooperative) and small flock sizes (non-cooperative).

Survival was lowest during the first 5 days post-fledging representing 53.3%. Once that juvenile starvation in rare in Taita Hills (Callens, 2012; Winckel, 2014) such result are better explained with high predation rates. As we see, mortality risk of post-fledging juveniles varied with age and probability of predation might be correlated with developmental behaviours occurring at different ages. During the first days, pulli remain near the ground, unable to fly quickly or long distances. In order to avoid predators, juveniles remain still and silent for long periods using specially the legs to jump from place to place. During the next 15 days, risk of predation decreased due to their much better (although not like parents) flying capabilities, what makes it easier to escape from the predators. 20 days after fledgling, flying capabilities seems to be as efficient as adult birds, enhancing their escape chances increasing ultimately their survival probabilities (Yackel Adams, Skagen et al., 2006; Tarwater and Brawn, 2010).

In the end of the 50 days, the post-fledgling survival probability of Cabanis Greenbul revealed to be relatively low (40%) in comparison to previous studies involving also tropical or Neotropical species (Cohen and Lindell, 2004; Brouwer, Richardson et al., 2006; Sankamethawee, Gale et al., 2009). For example, Brouwer *et al.* (2006) used the Seychelles Warbler (*Acrocephalus sechellensis*) as a model species and verified a survival probability of 0.61 (Brouwer, Richardson et al., 2006). The same result was reported by W. Sankamethawee et al. (2009) using the facultative cooperative breeder Puff-throated bulbul (*Alophoixus pallidus*) (Sankamethawee, Gale et al., 2009). *P. cabanisi* is considered to be a tropical bird with slow life history, characterized by much longer breeding seasons, smaller clutch size, high adult survival and high parental care (Tarwater and Brawn, 2010; Winckel, 2014). Such features are predicted to increase offspring survival (Tarwater and Brawn, 2010) although this effect was not confirmed on our study. I suggest that this outcome is the result of high habitat disturbance observed in Taita Hills (Wilder, Brooks et al., 1998; Chege and Bytebier, 2005; Pellikka, Lötjönen et al., 2009) what possibly gave rise to fragmented forest that negatively affected the juveniles survival rate (William D. Newmarka, 2011). Similar results were obtained by King et al. (2006) (King, Degraaf et al., 2006), who reported a positive relationship between vegetation structure and fledgling survival. In contrast, S. A. Rush et al. (2008) (Rush and Stutchbury, 2008) found no significantly difference in fledging survival between large and small forest fragments. Although non-significant, we observed different survival rates among fragments however, due to the lack of information related to habitat disturbance on each patch, we cannot analyse our results in an inter-fragments perspective.

Flock size was highly positively correlated with post fledging survival in both the studied periods. These results imply that on this population, as bigger the flock, as greater the post fledging survival. Once starvation is rare, we think that helpers, besides having an important role on feeding the juveniles and therefore lighten the load of the breeders, are also deeply involved in the defence against predators. Sorato, *et al.* (2012) found out that groups were more likely to encounter and be attacked by avian predators when dependent young were present. Furthermore, large groups were also more likely to encounter a predator, but less likely to be attacked by it (Sorato, Gullett et al., 2012). Beside this advantage, it is also likely that individuals living in groups are more efficient at detect early any intrude (Krause and Ruxton, 2002) and or confusing predator during their escape (Landeau and Terborgh, 1986). Moreover, Clutton-Brock, *et al.* (1999) found out that survival among the offspring of Mongoose (*Suricata suricatta*) increased together with the flock size, especially in areas of high predator density (Clutton-Brock, Gaynor et al., 1999). The observed stronger correlation during the second period, is in our perspective, especially due firstly to the fact that pulli are almost totally flightless during the first 5 days after fledged. *P. cabanisi* were never observed to mob predators therefore flock size will not make any difference upon an encounter with a predator during the first 5 days. Secondly, like explained above, after the 5th day juveniles have already some flying abilities. Although not perfect, such feature will allow them to take advantage of living in a large group by detecting earlier the presence of a predator.

Ptilochronology values showed to be also significantly correlated with post-fledgling survival. In practice, good habitat quality or good BF quality, will lead to a higher juvenile survival rate. Although we were not able to show any significant difference among or within fragments quality, this result confirms that, at a nest level, differences not only exist, as also significantly influence the post fledging survival of the chicks. Ridley et al. (2007), using the Arabian babbler (*Turdoides squamiceps*) concluded that environmental factors affect offspring survival from hatching to maturity (Ridley, 2007). Such influence might also be transmitted to the pulli indirectly, through the BF. A good habitat quality will lead the BF to a good nutritional state, allowing her in theory to have enough available energy to provide the juvenile(s) with high parental care. Fairbanks *et al.* (1995) analysed the maternal condition and the quality of maternal care in Vervet Monkeys (*Cercopithecus aethiops sabaeus*) and they conclude that mothers in marginal condition limited maternal care to restore their own health, often at the expense of infant mortality (Fairbanks and Mcguire, 1995).

Fluctuating asymmetry showed to be also have an impact on our offspring survival rate, although in the opposite direction that we were expected. According to our results, high number of fluctuating asymmetry positively influence the survival probability of our juveniles. In most investigations, FA is regarded as an individual based proxy for environmental and genetic stress effects (De Coster, Van Dongen et al., 2013) but this association cannot be made on our study. An important factor that was missing in our analysis was the incorporation of the measurement errors variance into our model. Such procedure eliminates errors caused by the observer and allow us to establish real differences in symmetry (Kotiaho, 2001) (Lens, 1999). Furthermore, some authors claim that FA measurements and statistical analysis are quite complex and that the DI variation is often too low leading to very weak correlation between developmental instability (DI) and FA and therefore not revealing differences in DI among individuals or meta-population (Dongen, 2006; De Coster, Van Dongen et al., 2013).

The past and current forest disturbance and fragmentation might have been responsible for the loss of suitable habitat for breeding of *P. cabanisi*. In general, environmental stress created novel selective pressure on our population, constraining therefore the possibility of independent breeding leading consequently to the delay of dispersal. Once our study species is a resident bird, non-migrant and therefore not morphologically adapt to fly long distances, the high fragmented terrain might also preclude the birds from disperse and find new breeding areas (Lens, Van Dongen et al., 2002). Once these occurred, the birds which remain in the natal territory might have been forced to give some compensation to the resident individuals avoiding being expulsed. High proportion of agricultural land and high human density (as verified in Taita Hills) carries over high rates of predation (Andr, xe et al., 1985). The best way of compensation was then better expressed through reducing this high predation risk, and group formation, particularly during breeding season was the key. By doing this, delayers were not only promoting higher survival rates of resident birds but also their self due to group augmentation benefit. Our findings are in line with Winckel, J. (2014) that states a higher prevalence of cooperative breeding behaviour in more fragmented and disturbed patches. Furthermore, if helpers would have any degree of kinship with resident birds, increasing the survival of breeder's offspring, it would increase even more their benefits of delaying their dispersal and cooperative breeding would be promoted among flocks. Unpublished data suggest that at least in some cases, cooperative breeding is kin-based, confirming therefore our theory. Even in a non-kin based society, helping could be advantageous in the way that learning and acquiring skills might lead to a higher reproductive success compared with novice breeders

(Komdeur, 1996). Moreover, helping unrelated individuals may increase the helper's chance of direct or future access to mates, in a way that would not be available to a floater (Cockburn, 1998).

Although not significantly, we found a negative relationship between growth bar width and flock size. Considering the size of the growth bars as an individual-based proxy for nutritional condition and consequently habitat quality, the previous observed relationship tell us that there are smaller flocks in better quality areas. Through this relationship we are able to tell that cooperative breeding might indeed be an adaptive response to low quality fragments. Additionally, Cabanis's Greenbul is a facultative cooperative breeder, meaning that not all individuals perform it, indicating that not always is advantageous to cooperate with outsiders. Such fact allow us to reject the hypothesis proposed by Port et al. (2011) that suggests greater direct advantage of groups over pairs or individuals in territorial contests because they can retain larger and/or better territories. If this was true, we would have found a positive correlation between habitat quality and flock size, and such did not happen (Port, Kappeler et al., 2011). The same relationship was observed between the incidence of cooperative breeding behaviour and growth bars width confirming our theory. We believe that a higher sample size might lead to stronger results that supports our theory.

Future research

In my opinion, the most prominent research related with this topic concerns the habitat/individual quality. Our results showed through ptilochronology, a significant correlation between habitat/individual quality and post-fledging survival. This give us only half of the information we need in order to understand what really influences the juvenile survival and therefore the population dynamics of our study species. With the purpose of completely answer this question it would be very important and crucial to disentangle habitat and individual quality from each other and verify which relationship exist between them. This would only be possible with the use of experimental works. Both concepts have been broadly used although often means different things for different people. Despite the efforts of ecologists and evolutionary biologists to explore among-individual heterogeneity in fitness, it is not clear how the concept of 'individual quality' relates to evolutionary theory (Wilson and Nussey, 2010), especially concerning cooperatively breeding populations. In my opinion, it would also be important to specify what exactly represent in Taita Hills a 'good quality patch'. Tom Callens (2012) emphasizes that improved forest quality may enhance local carrying capacities of some predator species leading therefore to

an overall negative impact on our population (Callens, 2012). On the other hand, Spanhove et al. (2013) described Taita Hills with an 'inverse edge-effect' (Spanhove, Callens et al., 2013). Accordingly, a smaller and more disturbed fragment normally described as a 'bad quality patch', might represent for *P. cabanisi* a good quality territory with less predators. Once that predation has proven to have such a high impact on this species, these knowledge would be essential to understand the impact of disturbance and generate predictions on the long-term viability of Cabanis's greenbul.

It would also be important to have a more accurate information about the individual quality of the helpers. This information would enlighten us about the possible reasons why does a bird become helper. For instance, it is possible that only low quality individuals delay their dispersal and independent reproduction once that they do not have at that moment, good enough physical conditions to perform this act.

Cooperative breeding might also be based in kin relationships. It is a priority to infer for this possibility, because such fact might change our current perspective of the life-history of this species. Once such information is obtained, we would have a cleanlier idea about the origin of this behaviour on this population as well as about the indirect fitness benefits of helping or even be able to explain the existence of lazy members on cooperatively breeding flocks. Additionally, such analysis could give insights of possible promiscuous behaviours existing within/among flocks. This last topic has been showed over the last years, to be of big complexity. Mulder, et al. (1996) proved that unexpectedly, 95% of the broods contained at least one young sired by extra-group fathers. Furthermore, they conclude that females control fertilization in superb fairy-wrens (*Malurus cyaneus*), by managing a trade-off between genes of high-quality males and parental care (Mulder, 1994). Cornwallis et al. (2010) demonstrated that "promiscuity reduces relatedness and hence disrupts selection for cooperation in family groups. Promiscuity is therefore an unifying explanatory variable in the transition to cooperative societies across species" (Cornwallis, West et al., 2010). If in Cabanis's greenbul extra-group paternity is common, then helper's indirect benefits may be much lower than estimated previously (Whittingham, Dunn et al., 1997). This situation was once described by Kingma et al. (2010) that showed that in Purple-crowned fairy-wren (*Malurus coronatus),* improvement of male breeder survival and enhanced productivity were more likely when fidelity was higher (Kingma, Hall et al., 2010). Such patterns help us understanding the mechanisms behind the evolution of cooperative breeding in this species.

In the course of this thesis, I proposed habitat fragmentation and human disturbance as strong ecological factors that drive(d) our species to its currently state. In order to confirm these suspicions, would be of major relevance to compare the reproductive strategies and reproductive success of populations living in intact forests and disturbed patches. Probably the East Usambara Mountains is the most suitable place to conduct this study. Such place contains a broad gradient of forest disturbance including sites where there has been minimal human disturbance, as big as 6790 ha (Newmark, 2006). Besides, it also belongs to the Eastern Arc Mountains complex, owing a relatively similar biodiversity, biogeography and climatic conditions as Taita Hills (Korfanta, Newmark et al., 2012).

Conclusion

In conclusion, flock size and growth bars width of the breeding female showed to be good indicators of juveniles post-fledging survival. Once we access the nutritional condition of the BF, or the maximum number of individuals present in one flock, we are able (in this population) to predict the fate of the pulli. In one hand, growth bars width is related with food availability and therefore habitat quality as well as the foraging capability/energy content of a specimen and therefore its individual quality. On another hand flock size is predicted to increase with the relative costs of dispersing and breed independently as well as with territory/individual quality. Individuals less capable to breed and/or territories with less available resources, might need bigger flock size in order to achieve the same reproductive success of the high individual/habitat quality.

For years that the Eastern Arc Mountains, especially Taita Hills, have been suffering from human disturbance. More than 98% of the original forest was damage or destroyed over the last 200 years. Among numerous others consequences, clearance for timber and agriculture followed by exotic plant species plantation, has led to an increase of predation risk. Such effect might constitute an important selection pressure on group living in cooperative species. Moreover, we suggest that cooperative breeding in this population emerged as an evolutionary adaptation to the negative human impact in this region.

Most of the studies addressing investigation in cooperative breeding systems where group members provide care to the offspring of others, do not consider the benefits of group augmentation. Our results are therefore of wide interest for the scientific community because through ptilochronology we were able for the first time to verify the relationship between

individual/environmental quality and cooperative incidence as well as its impact in the short-term post fledging survival of a tropical bird.

These results will help us to provide a better understanding of the impact of habitat/individual quality in the dynamics of this population, in particular because our study was based in a tropical species living in relatively unstable environment, due especially to high human disturbance and consequent forest fragmentation.

Despite the encouraging results we had, this thesis rouse even more questions about the life-history differences between tropical and temperate-zone species. Long-term studies might give us the answers we are looking for.

References

Aben, J., et al. (2012). "Effects of Matrix Composition and Configuration on Forest Bird Movements in a Fragmented Afromontane Biodiversity Hot Spot." Animal Conservation 15(6): 658-668.

Aerts, R., et al. (2010). "Woody Plant Communities of Isolated Afromontane Cloud Forests in Taita Hills, Kenya." Plant Ecology 212(4): 639-649.

Alan B. Franklin, D. R. A., R. J. Gutierrez, and Kenneth P. Burnham (2000). "Climate, Habitat Quality, and Fitness in Northern Spotted Owl Populations in Northwestern California." Ecological Monographs 70(4).

Allison, P. D. (1999). "Comparing Logit and Probit Coefficients across Groups." Sociological Methods & Research 28(2): 186-208.

Andr, et al. (1985). "Differences in Predation Pressure in Relation to Habitat Fragmentation: An Experiment." OIKOS 45(2): 273-277.

Arnold, K. E. and Owens, I. P. F. (1998). "Cooperative Breeding in Birds: A Comparative Test of the Life History Hypothesis." Proceedings of the Royal Society B: Biological Sciences 265(1398): 739-745.

Bailey, R. E. (1952). "The Incubation Patch of Passerine Birds." The Condor 54(3): 121-136.

Beentje, H. J. N. U., N. (1988). "An Ecological and Floristic Study of the Taita Hills, Kenya." Utafiti 1: 23-66.

Blackmore, C. J. and Heinsohn, R. (2007). "Reproductive Success and Helper Effects in the Cooperatively Breeding Grey-Crowned Babbler." Journal of Zoology 273(3): 326-332.

Bradshaw, C. J. A., Sodhi, N.S. & Brook, B.W. (2009). "Tropical Turmoil: A Biodiversity Tragedy in Progress." Front. Ecol. Environ. 7: 79–87.

Brooks, T., et al. (1998). "Avian Biogeography of the Taita Hills, Kenya." Journal of East African Natural History 87(1): 189-194.

Brouwer, L., et al. (2006). "The Role of Group Size and Environmental Factors on Survival in a Cooperatively Breeding Tropical Passerine." Journal of Animal Ecology 75(6): 1321-1329.

Burgess, J. S. a. N. (2015). "Eastern Africa: Central Tanzania, Extending into K." WWF.

Callens, T. (2012). "Genetic and Demographic Signatures of Population Fragmentation in a Cooperatively-Breeding Forest Bird from South-East Kenya. Phd Dissertation." Ghent University.

Callens, T., et al. (2011). "Genetic Signature of Population Fragmentation Varies with Mobility in Seven Bird Species of a Fragmented Kenyan Cloud Forest." Mol Ecol 20(9): 1829-1844.

Chege, J. and Bytebier, B. (2005). "Vegetation Structure of Four Small Forest Fragments in Taita Hills, Kenya." Journal of East African Natural History 94(1): 231-234.

Clutton-Brock, T. (2002). "Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates." Science 296(5565): 69-72.

Clutton-Brock, T. H., et al. (1999). "Predation, Group Size and Mortality in a Cooperative Mongoose, Suricata Suricatta." Journal of Animal Ecology 68(4): 672-683.

Cockburn, A. (1998). "Evolution of Helpinvg Behavior in Cooperatively Breeding Birds." Animal Behaviour.

Cockburn, A. and Russell, A. F. (2011). "Cooperative Breeding: A Question of Climate?" Curr Biol 21(5): R195-197.

Cohen, E. B. and Lindell, C. A. (2004). "Survival, Habitat Use, and Movements of Fledgling White-Throated Robins (Turdus Assimilis) in a Costa Rican Agricultural Landscape." The Auk 121(2): 404-414.

Cornwallis, C. K., et al. (2010). "Promiscuity and the Evolutionary Transition to Complex Societies." Nature 466(7309): 969-972.

Covas, R. and Griesser, M. (2007). "Life History and the Evolution of Family Living in Birds." Proceedings of the Royal Society B: Biological Sciences 274(1616): 1349-1357.

Crick, H. Q. P. (1992). "Load-Lightening in Cooperatively Breeding Birds and the Cost of Reproduction." Ibis 134: 56-61.

Davies, N. B. and Krebs, J. R. (1993). An Introduction to Behavioural Ecology, Wiley.

De Coster, G., et al. (2013). "Fluctuating Asymmetry and Environmental Stress: Understanding the Role of Trait History." PLoS One 8(3): 8.

Del Hoyo, J., Elliott, A. And Christie, D. A., Eds, 2005. Handbook of the Birds of the World. Vol 10. and Cuckoo-Shrikes to Thrushes. Lynx Edicions, B.

Dongen, S. V. (2006). "Fluctuating Asymmetry and Developmental Instability in Evolutionary Biology: Past, Present and Future." J Evol Biol 19(6): 1727-1743.

Drummond, H. and Ancona, S. (2015). "Observational Field Studies Reveal Wild Birds Responding to Early-Life Stresses with Resilience, Plasticity, and Intergenerational Effects." Auk 132(3): 563-576.

Dunn, P. O., et al. (1995). "Fairy-Wren Helpers Often Care for Young to Which They Are Unrelated." Proceedings of the Royal Society of London B: Biological Sciences 259(1356): 339-343.

Elderbrock, E. K., et al. (2012). "Problems with Using Ptilochronology to Measure the Growth and Nutritional Status of Nestling Bluebirds." The Condor 114(4): 823-830.

Fair, J. M., et al. (1999). "Growth, Developmental Stability and Immune Response in Juvenile Japanese Quails (Coturnix Coturnix Japonica)." Proceedings of the Royal Society B-Biological Sciences 266(1430): 1735-1742.

Fairbanks, L. A. and Mcguire, M. T. (1995). "Maternal Condition and the Quality of Maternal Care in Vervet Monkeys." Behaviour 132(9): 733-754.

Fehérvári, P., et al. (2014). "Hatching Rank Influences Nutritional Condition in the Common Buzzard: Evidence from Ptilochronology." Journal of Raptor Research 48(3): 280-284.

Fishpool, L. T., J. (2005). Cabanis's Greenbul (Phyllastrephus Cabanisi). In: Del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & De Juana, E. (Eds.) (2014). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. (Retrieved from Http://Www.Hbw.Com/Node/57993 on 19 May 2015).

Frasz, L. M., et al. (2013). "Effects of Experience and a Visual Aid on Ptilochronology." Journal of Ornithology 155(1): 319-322.

Gardner, T. A., et al. (2009). "Prospects for Tropical Forest Biodiversity in a Human-Modified World." Ecology Letters 12(6): 561-582.

Githiru, M. and Lens, L. (2004). "Using Scientific Evidence to Guide the Conservation of a Highly Fragmented and Threatened Afrotropical Forest." Oryx 38(04).

Githiru, M., et al. (2011). "Using Science to Guide Conservation: From Landscape Modelling to Increased Connectivity in the Taita Hills, Se Kenya." Journal for Nature Conservation 19(5): 263-268.

Githiru, M., et al. (2005). "Nest Predation in a Fragmented Afrotropical Forest: Evidence from Natural and Artificial Nests." biological Conservation 123(2): 189-196.

Green, A. J. (2001). "Mass/Length Residuals: Measures of Body Condition or Generators of Spurious Results?" Ecology 82.

Gregory, R. D., et al. (2004). "Bird Census and Survey Techniques." Bird ecology and conservation: 17-56.

Griesser, M., et al. (2006). "Reduced Mortality Selects for Family Cohesion in a Social Species." Proceedings of the Royal Society of London B: Biological Sciences 273(1596): 1881-1886.

Grubb, T. C. (2006). Ptilochronology Feather Time and the Biology of Birds, Oxford University Press.

Hanna Kokko, E. A. (2001). "The Evolution of Cooperative Breeding through Group Augmentation." Proceedings of the Royal Society B: Biological Sciences 268: 187-196.

Hatchwell, B. J. (2009). "The Evolution of Cooperative Breeding in Birds: Kinship, Dispersal and Life History." Philos Trans R Soc Lond B Biol Sci 364(1533): 3217-3227.

Hatchwell, B. J. (2009). "The Evolution of Cooperative Breeding in Birds: Kinship, Dispersal and Life History." Philosophical Transactions of the Royal Society B: Biological Sciences 364(1533): 3217-3227.

Hatchwell, B. J. and Komdeur, J. (2000). "Ecological Constraints, Life History Traits and the Evolution of Cooperative Breeding." Anim Behav 59(6): 1079-1086.

Hooper, D. U., et al. (2005). "Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge." Ecological Monographs 75(1): 3-35.

Husemann, M., et al. (2015). "Post-Fragmentation Population Structure in a Cooperative Breeding Afrotropical Cloud Forest Bird: Emergence of a Source-Sink Population Network." Mol Ecol 24(6): 1172-1187.

International, B. (2015). "Important Bird Areas Factsheet: Taita Hills Forests. ." BirdLife International.

International, B. (2015). "Species Factsheet: Phyllastrephus Cabanisi.".

Jackson, S. F. a. W. M. (1990). "Univariate Metrics Are Not Adequate to Measure Avian Body Size." The Auk 107.

Johnson, M. D. (2007). "Measuring Habitat Quality: A Review." The Condor 109(3): 489-504.

King, D. I., et al. (2006). "Habitat Selection and Habitat-Specific Survival of Fledgling Ovenbirds (Seiurus Aurocapilla)." Journal of Zoology 269(4): 414-421.

Kingma, S. A., et al. (2010). "Multiple Benefits of Cooperative Breeding in Purple-Crowned Fairy-Wrens: A Consequence of Fidelity?" Journal of Animal Ecology 79(4): 757-768.

Knierim, U., et al. (2007). "Fluctuating Asymmetry as an Animal Welfare Indicator — a Review of Methodology and Validity." Physiology & Behavior 92(3): 398-421.

Komdeur, J. (1996). "Influence of Helping and Breeding Experience on Reproductive Performance in the Seychelles Warbler: A Translocation Experiment." Behavioral Ecology 7.

Korfanta, N. M., et al. (2012). "Long-Term Demographic Consequences of Habitat Fragmentation to a Tropical Understory Bird Community." Ecology 93(12): 2548-2559.

Kotiaho, J. L. T. J. S. (2001). Encyclopedia of Life Sciences: Fluctuating Asymmetry, Macmillan Publishers Ltd, Nature Publishing Group.

Krause, J. and Ruxton, G. D. (2002). Living in Groups, Oxford University Press.

Landeau, L. and Terborgh, J. (1986). "Oddity and the 'Confusion Effect' in Predation." Animal Behaviour 34(5): 1372-1380.

Langen, T. A. (1996). "Skill Acquisition and the Timing of Natal Dispersal in the White-Throated Magpie-Jay, Calocitta Formosa." Animal Behaviour.

Lens, L. and Van Dongen, S. (2000). "Fluctuating and Directional Asymmetry in Natural Bird Populations Exposed to Different Levels of Habitat Disturbance, as Revealed by Mixture Analysis." Ecology Letters 3(6): 516-522.

Lens, L., et al. (2002). "Avian Persistence in Fragmented Rainforest." Science 298(5596): 1236-1238.

Lens, L., Van Dongen, S., Wilder, C. M., Brooks, T. M. & Matthysen, E. (1999). "Fluctuating Asymmetry Increases with Habitat Disturbance in Seven Bird Species of a Fragmented Afrotropical Forest." Proceedings of the Royal Society of London Series B-Biological Sciences 266: 1241-1246

Loock, D. V. D. (2012). "Cooperative Breeding Strategies in a Fragmented Population of a Tropical Forest Passerine." Gent univeristy.

Lovett, J. C., S.K. Wasser (1993). "Biogeography and Ecology of the Rain Forests of Eastern Africa." Cambridge: Cambridge University Press.

Mcnamara, J. M. H., Alasdair I (1996). "State Dependent Life Histories." Nature 380: 215.

Meade, J., et al. (2010). "Consequences of 'Load-Lightening' for Future Indirect Fitness Gains by Helpers in a Cooperatively Breeding Bird." J Anim Ecol 79(3): 529-537.

Morrison, M. L., et al. (2012). Wildlife-Habitat Relationships: Concepts and Applications, Island Press.

Mulder, R. A., Dunn, P. O., Cockburn, A., Lazenbycohen, K. A., Howell, M. J. (1994). "Helpers Liberate Female Fairy-Wrens from Constraints on Extra-Pair Mate Choice." Proceedings of the Royal Society B-Biological Sciences 255(1344): 223-229.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., Kent, J. , : . (2000). "Biodiversity Hotspots for Conservation Priorities." Nature 403: 853-858.

Naef-Daenzer, B. (2007). "An Allometric Function to Fit Leg-Loop Harnesses to Terrestrial Birds." Journal of Avian Biology 38: 404-407.

Naef-Daenzer, B. E. A. (2005). "Miniaturization (0.2g.) and Evaluation of Attachment

Techniques of Telemetry Transmitters." J. Exp. Biol. 208: 4063-4068.

Newmark, W. D. (2006). "A 16-Year Study of Forest Disturbance and Understory Bird Community Structure and Composition in Tanzania

Un Estudio De 16 Años De La Perturbación De Bosques Y La Estructura Y Composición De La Comunidad De Aves De Sotobosque En Tanzania." Conservation Biology 20(1): 122-134.

Okuliarova, M., et al. (2010). "Yolk Testosterone and Corticosterone in Hierarchical Follicles and Laid Eggs of Japanese Quail Exposed to Long-Term Restraint Stress." Gen Comp Endocrinol 165(1): 91-96.

Owens, A. (1998). "Cooperative Breeding in Birds: A Cooperative Test of the Life History Hypothesis." ProRSocLondB 265.

Palmer, A. R. S., C. (1986). "Fluctuating Asymmetry: Measurement, Analysis and Patterns." A. Rev. Ecol.Syst. 17: 391-421.

Pellikka P., Y. J., Clark B. (Eds.) (2004). " Taita Hills and Kenya, 2004. Seminar, Reports and Journal of a Field Excursion to Kenya. Expedition Reports of the Department of Geography, University of Helsinki." 40: 31-38.

Pellikka Pke, L. M., Sijander M, Lens L. (2009). "Airborne Remote Sensing of Spatiotemporal Change (1955-2004) in Indigenous and Exotic Forest Cover in the Taita Hills, Kenya." International Journal of Applied Earth Observation and Geoinformation 11: 221-232.

Pellikka, P. K. E., et al. (2009). "Airborne Remote Sensing of Spatiotemporal Change (1955–2004) in Indigenous and Exotic Forest Cover in the Taita Hills, Kenya." International Journal of Applied Earth Observation and Geoinformation 11(4): 221-232.

Port, M., et al. (2011). "Communal Defense of Territories and the Evolution of Sociality." Am Nat 178(6): 787-800.

Prell, W. L., W.H. Hutson, D.F. Williams, A. Be, K. Geitzenauer and B. Molfino (1980). "Surface Circulation of the Indian Ocean During the Last Glacial Maximum, Approximately 18,000 Yr Bp." Quaternary Research 14: 309-336.

Rappole, J. H., Tipton, A. (1990). "New Harness Design for Attachment of Radio Transmitters to

Small Passerines." Journal of Field Ornithology 62: 335-337.

Ridley, A. R. (2007). "Factors Affecting Offspring Survival and Development in a Cooperative Bird: Social, Maternal and Environmental Effects." Journal of Animal Ecology 76(4): 750-760.

Riehl, C. (2013). "Evolutionary Routes to Non-Kin Cooperative Breeding in Birds." Proceedings of the Royal Society of London B: Biological Sciences 280(1772).

Robinson, S. K. (1995). "Regional Forest Fragmentation and the Nesting Success of Migratory Birds." Science.

Rolstad, J. (1991). "Consequences of Forest Fragmentation for the Dynamics of Bird Populations: Conceptual Issues and the Evidence." Biological Journal of the Linnean Society 42: 149–163.

Rubenstein, D. R. (2011). "Spatiotemporal Environmental Variation, Risk Aversion, and the Evolution of Cooperative Breeding as a Bet-Hedging Strategy." Proc Natl Acad Sci U S A 108: 10816-10822.

Rush, S. A. and Stutchbury, B. J. M. (2008). "Survival of Fledgling Hooded Warblers (Wilsonia Citrina) in Small and Large Forest Fragments." The Auk 125(1): 183-191.

Sandercock, B. K., et al. (2000). "Survival Rates of a Neotropical Parrot: Implications for Latitudinal Comparisons of Avian Demography." Ecology 81(5): 1351-1370.

Sankamethawee, W., et al. (2009). "Post-Fledgling Survival of the Cooperatively Breeding Puff-Throated Bulbul (Alophoixus Pallidus)." The Condor 111(4): 675-683.

Santos, E. S. A. and Macedo, R. H. (2011). "Load Lightening in Southern Lapwings: Group-Living Mothers Lay Smaller Eggs Than Pair-Living Mothers." Ethology 117(6): 547-555.

Sorato, E., et al. (2012). "Effects of Predation Risk on Foraging Behaviour and Group Size: Adaptations in a Social Cooperative Species." Animal Behaviour 84(4): 823-834.

Spanhove, T., et al. (2013). "Nest Predation in Afrotropical Forest Fragments Shaped by Inverse Edge Effects, Timing of Nest Initiation and Vegetation Structure." Journal of Ornithology 155(2): 411-420.

Stacey, P. B. a. L., J. D. (1987). "Territory Quality and Dispersal Options in the Acorn Woodpecker, and a Challenge to the Habitat Saturation Model of Cooperative Breeding. ." Am. Nat. 130: 654-676.

Talloen, W., et al. (2008). "Feather Development under Environmental Stress: Lead Exposure Effects on Growth Patterns in Great Tits Parus Major." Bird Study 55: 108-117.

Tarwater, C. E. and Brawn, J. D. (2010). "The Post-Fledging Period in a Tropical Bird: Patterns of Parental Care and Survival." Journal of Avian Biology 41(4): 479-487.

Tarwater, C. E., et al. (2011). "Pre-Reproductive Survival in a Tropical Bird and Its Implications for Avian Life Histories." Ecology 92(6): 1271-1281.

Thijs, K. W., et al. (2014). "Potential Tree Species Extinction, Colonization and Recruitment in Afromontane Forest Relicts." Basic and Applied Ecology 15(4): 288-296.

Vangestel, C. (2006). "Ptilochronology Protocol."

Vangestel, C. (2011). "Relating Phenotipic and Genetic Variation to Urbanization in Avian Species: A Case Study in House Sparrow (*Passer Domesticus*) - Phd Dissertation."

Vangestel, C., et al. (2013). "Sex-Biased Dispersal at Different Geographical Scales in a Cooperative Breeder from Fragmented Rainforest." PLoS One 8(8): e71624.

Vitz, A. C. and Rodewald, A. D. (2011). "Influence of Condition and Habitat Use on Survival of Post-Fledging Songbirds." The Condor 113(2): 400-411.

Wagura, L. (2014). A Guide to Taita Hills Unique Natural History.

Walter D. Koenig, J. L. D. (2004). Ecology and Evolution of Cooperative Breeding in Birds, Cambrige University Press.

Wendeln, H. a. B., P. H. (1999). "Effects of Parental Quality and Effort on the Reproduction of Common Terns." Journal of Animal Ecology 68: 205–214.

Whittingham, L. A., et al. (1997). "Relatedness, Polyandry and Extra-Group Paternity in the Cooperatively-Breeding White-Browed Scrubwren (Sericornis Frontalis)." Behavioral Ecology and Sociobiology 40(4): 261-270.

Wilder, C., et al. (1998). "Vegetation Structure and Composition of the Taita Hills Forests." Journal of East African Natural History 87(1): 181-187.

William D. Newmarka, A. T. R. S. (2011). "Habitat Fragmentation Reduces Nest Survival in an Afrotropical Bird Community in a Biodiversity Hotspot." PNAS 108.

Wilson, A. J. and Nussey, D. H. (2010). "What Is Individual Quality? An Evolutionary Perspective." Trends in Ecology & Evolution 25(4): 207-214.

Winckel, J. V. (2014). How Do Helpers Pay the Rent? Assessing Helper Effects in a Fragmented Population of a Tropical Cooperative Breeder. G. Univeristy.

Witter, J. P. S. a. M. S. (1994). "Food, Feathers and Fluctuating Asymmetry." Proceedings of the Royal Society B: Biological Sciences 255: 147-152.

Yackel Adams, A. A., et al. (2006). "Modeling Post-Fledging Survival of Lark Buntings in Response to Ecological and Biological Factors." Ecology 87(1): 178-188.

Young, E. C. (1998). "Dispersal from Natal Territories and the Origin of Cooperatively Polyandrous Breeding Groups in the Brown Skua." The Condor 100(2): 335-342.